

ALVAREZSAURIDAE, CRETACEOUS BASAL BIRDS FROM PATAGONIA AND MONGOLIA

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Alvarezsauridae represents a clade of bizarre birds with extremely reduced but powerful forelimbs. Twenty synapomorphic features shared by *Patagonykus*, *Alvarezsaurus* and *Mononykus* supports Alvarezsauridae as a monophyletic group of avialan theropods. Diagnostic characters, mainly referred to vertebral, forelimb, pelvic and hindlimb anatomy, emerge from a cladistic analysis of 74 derived features depicting Alvarezsauridae as the sister taxon of the avialian clade Ornithothoraces. Since the origin and early diversification of the Alvarezsauridae probably took place during, or prior to, the Early Cretaceous, their common presence in Patagonia and Mongolia reflects a wider geographical distribution over the world, prior to the development of major geographical barriers between Laurasia and Gondwana during Aptian to Cenomanian times. □ *Alvarezsauridae, Patagonykus, Mononykus, birds.*

Los Alvarezsauridae constituyen un clado de extrañas aves basales, caracterizados por sus miembros anteriores extremadamente reducidos, aunque proporcionalmente robustos. Veinte sinapomorfías compartidas por *Patagonykus*, *Alvarezsaurus* y *Mononykus* sustentan la hipótesis que Alvarezsauridae conforma un grupo monofilético de terópodos avialanos. Los caracteres diagnósticos de Alvarezsauridae se refieren principalmente a la columna vertebral, miembros anteriores y posteriores, y pélvis, y emergen de un análisis cladístico de 74 rasgos derivados muestran a Alvarezsauridae como el grupo hermano del clado avialiano Ornithothoraces. En base a las hipótesis filogenéticas propuestas, se estima que el origen y temprana radiación de los alvarezsáuridos habría ocurrido, al menos, durante el Cretácico temprano. Este dato permite suponer que estos terópodos se habrían dispersado en varios continentes (p.ej., América del Sur, América del Norte, y Asia) antes que se instalaran barreras geográficas de importancia entre Laurasia y Gondwana durante el Cretácico 'Medio'.

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Alvarezsauridae (Bonaparte, 1991) is a clade of bizarre avialan theropods from Upper Cretaceous rocks of Mongolia and Patagonia. At present they are known by three different species: the Patagonian *Alvarezsaurus calvoi* (Bonaparte, 1991), *Patagonykus puertai* gen. et sp. nov. (Novas, in press a) and the Mongolian *Mononykus olecranus* (Perle et al., 1993, 1994; Chiappe et al., this volume). By far, the latter species is the best represented one, being known from complete cranial and postcranial skeletons (Perle et al., 1993; 1994; Chiappe et al., this volume). On the contrary, the South American taxa *Patagonykus* and *Alvarezsaurus* are not completely known and the most serious lack of information refers to the skull. Nevertheless, the available osteological material pertaining to the Patagonian forms is informative, allowing recognition of autapomorphic features diagnostic of each of the Patagonian species. Although incompletely represented, *Patagonykus* and *Alvarezsaurus* are significant phylogenetically since they

retained the plesiomorphic state for several features that *Mononykus* shares with birds, more derived than *Archaeopteryx*.

Better documented now than they were five years ago (Bonaparte, 1991), some aspects of the phylogenetic relationships of the alvarezsaurids are now better understood. For example, it is now clear that Alvarezsauridae does not constitute a theropod branch of uncertain relationships, as originally interpreted by Bonaparte (1991); on the contrary, they are deeply internested within Tetanurae, Coelurosauria and Maniraptora because they exhibit hypapophyses on vertebrae from the cervicothoracic region, semilunate carpal, retroverted pubis, posterodorsal margin of ilium ventrally curved in lateral view and pubic foot cranially reduced (Gauthier, 1986).

There are, however, several features that make these theropods particularly interesting: first, they exhibit peculiar adaptations in the forelimbs and vertebral column, the functional significance of which is controversial (e.g., Perle et al., 1993,

1994; Ostrom, 1994); second, alvarezsaurids share with birds several apomorphic resemblances, more derived than *Archaeopteryx*, raising new questions about the early evolution of birds (Perle et al., 1993, 1994; Chiappe et al., this volume); third, alvarezsaurids are known from distant Upper Cretaceous localities of the world (e.g., Patagonia and Mongolia) and thus are interesting from a palaeobiogeographical point of view.

ABBREVIATIONS. AMNH, American Museum of Natural History, New York; BSP, Bayerische Staatssammlung für Paläontologie, Munich; CM, Carnegie Museum of Natural History, Pittsburgh; HMN MB, Humboldt Museum für Naturkunde, Berlin; GI, Geological Institute, Mongolian Academy of Sciences, Ulan Bator; MACN, Museo Argentino de Ciencias Naturales 'B. Rivadavia', Buenos Aires; MCZ, Museum of Comparative Zoology, Cambridge; MLP, Museo de La Plata, La Plata; MUCPV, Museo de Ciencias Naturales, Universidad Nacional del Comahue, Neuquén; PVL, Paleontología de Vertebrados, Fundación 'Miguel Lillo', San Miguel de Tucumán; PVPH, Paleontología Vertebrados, Museo Municipal 'Carmen Funes', Plaza Huinul, Neuquén; PVSJ, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan; USNM, United States National Museum, Washington, DC; YPM, Yale Peabody Museum, New Haven.

MATERIALS AND METHODS

MATERIAL EXAMINED. A comparative study of the holotypes of *Patagonykus puertai* (PVPH 37), *Alvarezsaurus calvoi* (MUCPV 54) and *Mononykus olecranus* (GI N107/6 cast) was conducted. The following specimens were also studied: *Albertosaurus libratus* (AMNH 5468), *Alectrosaurus olseni* (AMNH 6554), *Allosaurus fragilis* (AMNH 5767), *Archaeopteryx lithographica* (HMN MB 1880/81 and casts of London and Eichstätt specimens), *Archaeornithomimus asiaticus* (AMNH 6566, 6567, 6570), *Caiman latirostris* (pers. collection), *Compsognathus longipes* (BSP AS I 536), *Deinonychus antirrhopus* (AMNH 3015, MCZ 4371, YPM 5205, 5206, 5236), *Herrerasaurus ischigualastensis* (PVSJ 373), *Iberomesornis romerali* (MACN unnumbered cast), *Meleagriscus gallopavo* (pers. collection), *Mussaurus patagonicus* (MLP-68-III-27-1), *Ornitholestes hermani* (AMNH 619), *Ornithomimus velox* (AMNH 5355), *Ornithomimus sedens* (USNM 2164) and *Piatnitzkysaurus floresii* (MACN-CH 895).

ANATOMICAL TERMINOLOGY. I follow the terminology of Clark, 1993. 'Cranial' and

'caudal' are used here in place of 'anterior' and 'posterior', respectively.

SYSTEMATIC NOMENCLATURE. I ascribe to the notion of phylogenetic (node-based or stem-based) definitions for all taxa (de Queiroz & Gauthier, 1994). Aves is defined to encompass all the descendants of the most recent common ancestor of Ratitae, Tinami and Neognathae (Gauthier, 1986); Avialae includes *Archaeopteryx lithographica*, Aves and their most recent common ancestor; Maniraptora includes all those theropods more closely related to Aves than to the Ornithomimidae (Gauthier, 1986). With respect to Maniraptora, I am not following the synapomorphy-based definition given by Holtz (1994), who has also included ornithomimids and tyrannosaurids within Maniraptora on the assumption that the ancestors of these two taxa also possessed the diagnostic features of Maniraptora (e.g., raptorial manus, etc.). The node-based definition originally given by Gauthier (1986:30) perfectly fits to the clade formed by Dromaeosauridae plus Avialae, even accepting the monophyly of Arctometatarsalia (= Elmisauridae + *Avimimus* + Tyrannosauridae + Troodontidae + Ornithomimosauria); sensu Holtz, 1994).

SYSTEMATIC PALAEONTOLOGY

Basic information on the new taxon *Patagonykus puertai* is provided here. A detailed anatomical description and discussion of the automorphies diagnosing this species are given elsewhere (Novas, in press a).

COELUROSAURIA Huene, 1920
 MANIRAPTORA Gauthier, 1986
 AVIALAE Gauthier, 1986
 METORNITHES Perle et al., 1993
 ALVARESAURIDAE Bonaparte, 1991

Patagonykus gen. nov.

Patagonykus puertai gen. et sp. nov.

MATERIAL EXAMINED. HOLOTYPE PVPH 37, two incomplete dorsal vertebrae, incomplete sacrum, two proximal and two distal caudal vertebrae; incomplete left and right coracoids, proximal and distal ends of both humeri, right proximal portions of ulna and radius, and distal portion of left ulna, articulated carpometacarpus and first phalanx of digit I of the right manus; incomplete ungual phalanx probably corresponding to digit I; portions of ilia, proximal ends of ischia, and portions of pubes; proximal and distal por-

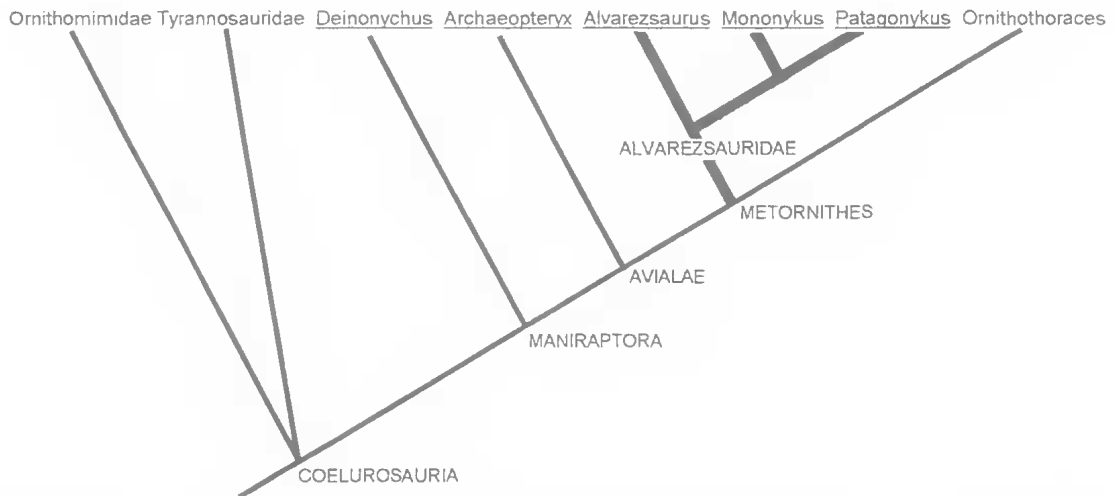


FIG. 1. Cladogram depicting the phylogenetic relationships among *Patagonykus*, *Alvarezsaurus* and *Mononykus*, and five immediate outgroups.

tions of right femur, and distal end of the left; proximal and distal ends of both tibiae, fused with proximal tarsals; metatarsals II and III fused to distal tarsals III; several pedal phalanges.

HORIZON AND AGE. Portezuelo Member of the Río Neuquén Formation (possibly Turonian, Late Cretaceous; Cruz et al., 1989), Sierra del Portezuelo, 22km west of Plaza Huincul City, Neuquén Province, NW Patagonia, Argentina. The quarry is situated 500m NW of National Route 22.

DIAGNOSIS. *Patagonykus puertai* is an alvarezsaurid avialian theropod diagnosed by the following: postzygapophyses in dorsal vertebrae with ventrally curved, tongue-shaped lateral margin; dorsal, sacral and caudal vertebrae with a bulge on the caudal base of the neural arch; humeral articular facet of coracoid transversely narrow; internal tuberosity of humerus subcylindrical, wider at its extremity rather than in its base; humeral entepicondyle conical and strongly projected medially; first phalanx of manual digit I with proximomedial hook-like processes; ectocondylar tuber of femur rectangular in distal view.

PHYLOGENETIC RESULTS

Seventy four derived features were coded as binary and their distribution examined in three terminal taxa and five outgroups (see Appendix). The data matrix was subjected to parsimony analysis using the implicit enumeration (ie) com-

mand in HENNIG 86 (version 1.5) by J.S. Farris (1988). A single most parsimonious tree was obtained (Fig. 1), with a length of 102 steps, a consistency index of 0.72 and a retention index of 0.74. This tree depicts Alvarezsauridae as the sister group of Ornithothoraces, but it must be emphasised that the tree supporting Alvarezsauridae outside Avialae (namely as the sister taxon of *Deinonychus* plus Avialae) differs in five evolutionary steps (characters listed in the Appendix). Until more evidence becomes available, I will consider alvarezsaurids as birds (e.g., avialians more derived than *Archaeopteryx*), in agreement with Perle et al. (1993, 1994) and Chiappe et al. (this volume).

OUTGROUP RELATIONSHIPS. The following taxa have been chosen for outgroup comparisons: Ornithothoraces, *Archaeopteryx*, *Deinonychus*, Tyrannosauridae and Ornithomimidae. Although there is a diversity of opinion about the phylogenetic arrangement of the terminal taxa, there is agreement among authors (e.g., Bakker et al., 1988; Novas, 1991; 1992; Holtz, 1994) that the Tyrannosauridae are more closely related to Ornithomimidae, Dromaeosauridae, Aves and other coelurosaurs, than to *Allosaurus* (contra Gauthier, 1986; Molnar et al., 1990). Another point of consensus is that Dromaeosauridae and Avialae form a clade (e.g., Maniraptora; Gauthier, 1986; Novas, 1991; 1992; Holtz, 1994).

In reference to the Avialae, the available data supports Alvarezsauridae as the sister taxon of Ornithothoraces, with *Archaeopteryx* as the out-

group (Perle et al., 1993, 1994; Chiappe et al., this volume).

TERMINAL TAXA. *Patagonykus puertai*, *Alvarezsaurus calvoi* and *Mononykus olecranus* were chosen as operational taxonomic units (OTU's) for parsimony analysis. The latter two taxa are diagnosed below on the basis of apomorphic characters, which are numbered and preceded by a letter identifying their presence in the corresponding taxon (A, *Alvarezsaurus*; M, *Mononykus*).

Alvarezsaurus calvoi Bonaparte, 1991. This taxon was originally diagnosed by Bonaparte (1991) on the basis of several features, some of which are problematic. For example, presence of 'cervical pleurocoels ... 5 or 6 sacrals ... ilium low and long ... unfused metatarsals and tarsals ... astragalus with wide condyles ... metatarsal III narrower in caudal view respect to the remaining metatarsals ... metatarsal IV greater proximally than the other metatarsals' are all characters widely distributed within Tetanurae (Gauthier, 1986), and clearly none of these features is autapomorphic for *Alvarezsaurus calvoi*. Other features (e.g., cranial sacrals with a slight axial depression on ventral surface; ilium with postacetabular blade greater than the preacetabular one) are widely — and unevenly — distributed among several non-avian and avian taxa and their status is difficult to verify. Other characters originally included in the diagnosis of this taxon (Bonaparte, 1991), such as 'neural spines vestigial in cervical and cranial dorsal vertebrae' and 'caudal sacrals with narrow ventral margin' are features also present in *Mononykus* and *Patagonykus* and are better interpreted as diagnostic of the Alvarezsauridae. Bonaparte has also listed the small size of the specimen as a diagnostic feature of *Alvarezsaurus*. However, the lack of fusion of the centra and respective neural arches of the cervical vertebrae, as well as the unfused centra of the sacrals, reveal that the holotype specimen of *Alvarezsaurus calvoi* was an immature individual that probably did not reach its maximum body size.

Restudy of the partial skeleton of *Alvarezsaurus calvoi* (MUCPV 54) allowed recognition of the following autapomorphies:

A1) Cervical centra amphicoelous (Fig. 2). Bonaparte (1991) originally recognised this character as diagnostic of *Alvarezsaurus*. This condition sharply contrasts with that present in the remaining Tetanurae (including *Mononykus*), in which the cranial articular surfaces of cervical

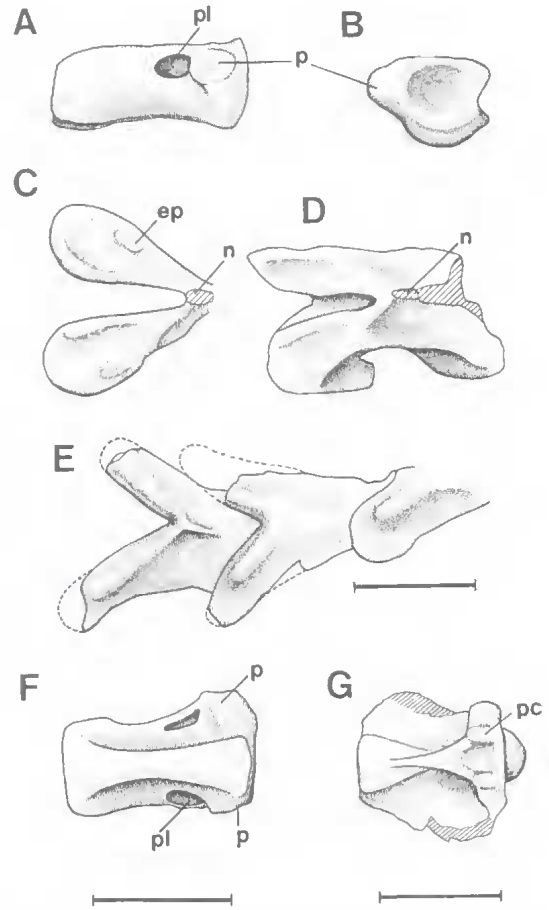


FIG. 2. Cervical vertebrae of Alvarezsauridae. A-D, F, *Alvarezsaurus calvoi* (MUCPC 54). A, B, F, cervical ?5th. D, 7th. C, 8th. E, G, *Mononykus olecranus* (GI N107/6 cast). E, ?6th to ?8th. G, 9th. (A, lateral; B, cranial; C, D, E, dorsal; F, G, ventral views). ep=epiphysis, n=neural spine, p=parapophysis, pc=processus caroticus, pl=pleurocoel; scale = 10mm.

centra are flat or convex. Procoelous cervical centra are also present in Ornithomimidae (e.g., *Archaeornithomimus* AMNH 6566, 6567, 6570).

A2) Cervical postzygapophyses dorsoventrally flattened, paddle-shaped in dorsal view, and with a pair of strong craniocaudal ridges (Fig. 2). *Alvarezsaurus* exhibits paddle-shaped, craniocaudally elongate postzygapophyses on cervical vertebrae (Bonaparte, 1991). This condition contrasts with other theropods (e.g., *Piatnitzky-saurus*, *Archaeornithomimus*, *Ornitholestes*, *Deinonychus*) in which the postzygapophyses are rectangular, not constricted at their bases, and with a convex dorsal surface bearing a prominent

epiphysis. In the caudal cervicals of *Alvarezsaurus* the postzygapophyses exhibit a strong, craniocaudally-oriented buttress running along the medial margin. This condition is seen in cervicals 7 to 9, but in cervicals 7 and 8 a lateral crest is also present, bounding a shallow basin over the dorsal surface of the postzygapophyses. This condition of the dorsal surface of the postzygapophyses contrasts with that present in other theropods, including *Mononykus* (GI N 107/6) in which the dorsal surface of the cervical postzygapophyses is smooth and transversely convex.

A3) Length of distal caudals more than 200% of the length of proximal caudals. In *Alvarezsaurus* (MUCPV 54) the centrum of the distalmost preserved caudal (presumably corresponding to the region of caudals 15 through 18), is 213% of the length of the most proximally preserved caudal. This condition resembles that of *Archaeopteryx* (Wellnhofer, 1974; 1988; 1993), in which the longest tail vertebrae (caudals 12 and 13) represents 185 to 287% of the length of the proximal caudal vertebrae (caudals 1 through 3). The elongation of the distal caudal segments in *Alvarezsaurus* sharply contrast with the proportions seen in non-avian maniraptorans (e.g., *Ornitholestes*, *Sinornithoides*, *Deinonychus*; Osborn, 1917; Ostrom, 1969; Russell & Dong, 1993b) in which the length of the distal caudals represents no more than 175% the length of the proximal caudals. *Alvarezsaurus* also differs from other alvarezsaurids, in which the length of caudal vertebrae remains more or less similar along the tail (e.g., *Mononykus*; Perle et al., 1994), or they are considerably smaller than the proximal ones, as in *Patagonykus* (PVPH 37). As for the Ornithothoraces, the distal caudal vertebrae are uniformly short (e.g., *Baptornis*, *Hesperornis*, *Ichthyornis*, *Patagopteryx*; Marsh, 1880; Martin

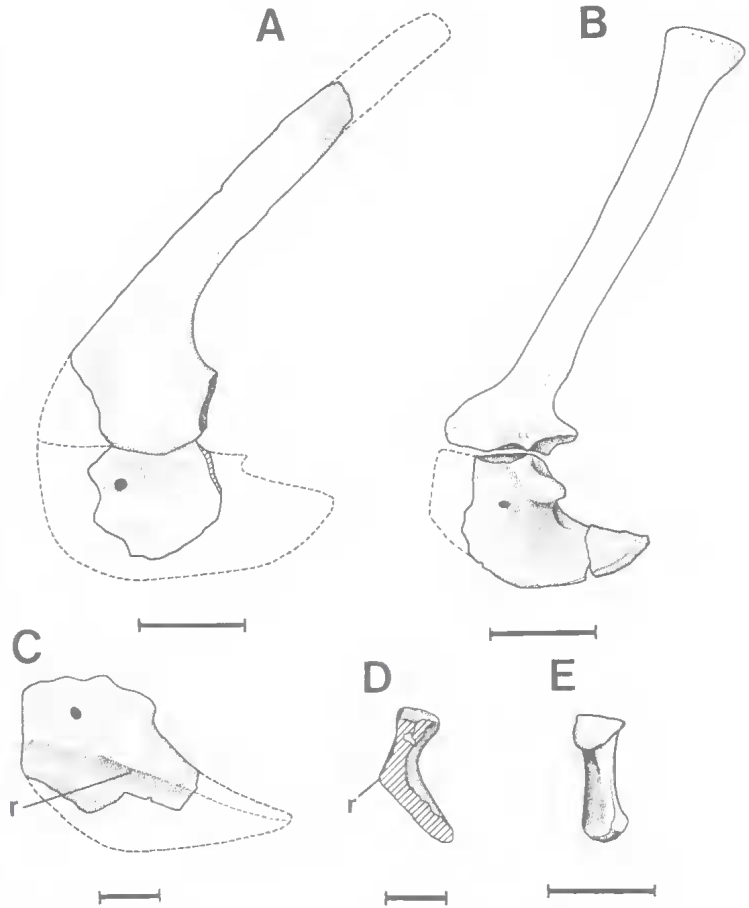


FIG. 3. Pectoral girdle of alvarezsaurids. A, *Alvarezsaurus calvoi* (modified from Bonaparte, 1991). B, E, *Mononykus olecranus* (GI N107/6 cast). C, D, *Patagonykus puertai* (composite reconstruction based on left and right coracoids of PVPH 37). (A, B, C, left lateral view of scapula and coracoid; D, E, caudal view of left coracoid). r=craniocaudal ridge, scale = 20mm.

& Tate, 1976; Alvarenga & Bonaparte, 1992), but this condition can not be easily considered ancestral for the clade, since in basal ornithothoracines (e.g., *Iberomesornis*, *Sinornis*; Sanz et al., 1988; Sereno & Rao, 1992) the distal caudals are strongly fused forming a pygostyle, preventing measurement of the length of each vertebral segment.

A4) Scapular blade slender and reduced (Fig. 3). Bonaparte (1991) included this feature in his original diagnosis. Although the distal end of the scapula of *Alvarezsaurus* is broken off, the cranial and caudal margins of the blade tend to converge distally, suggesting the lack of a distal expansion as present in other theropods (e.g., *Mononykus*, *Archaeopteryx*, *Tyrannosaurus*, *Allosaurus*;

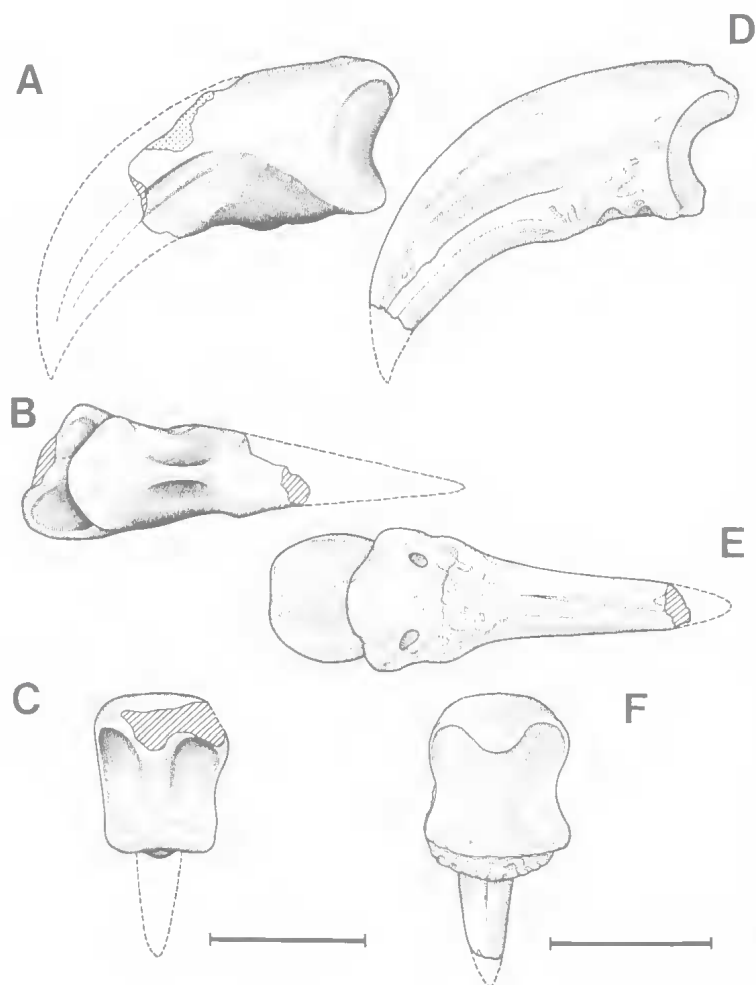


FIG. 4. Ungual phalanx of first manual digit of Alvarezsauridae. A, B, C, *Alvarezsaurus calvoi* (MUCPC 54). D, E, F, *Mononykus olecranus* (GI N107/6). (A, D, lateral; B, E, ventral; C, F, proximal views). Scale = 10mm.

Osborn, 1905; Madsen, 1976; Ostrom, 1976a; Perle et al., 1994). The scapula of *Alvarezsaurus* seems to be more slender than that of *Mononykus* (Perle et al., 1994), a conclusion that emerges when the scapula is compared with other skeletal elements: for example, in *Alvarezsaurus* (Bonaparte, 1991) the scapula represents 47% of the craniocaudal length of the iliac blade, instead in *Mononykus* (Perle et al., 1994) the scapula represents 86% of the craniocaudal length of the ilium.

A5) Ungual phalanx of digit I ventrally keeled (Fig. 4). Revision of the holotype specimen of *Alvarezsaurus calvoi* (MUCPV 54) allowed identification of a manual ungual phalanx, originally

undescribed by Bonaparte (1991). This phalanx is remarkably similar to that of *Mononykus* (see character 22), although in *Alvarezsaurus* the first manual ungual exhibits a strongly developed ventral keel on its proximoventral surface. By contrast, manual claws of most theropods (e.g., *Allosaurus*, *Ornithomimus*, *Deinonychus*, *Patagonykus*, *Mononykus*; Marsh, 1896; Ostrom, 1969; Madsen, 1976; Perle et al., 1994) this keel is absent and the ventral ungual surface is transversely rounded or flattened.

Mononykus olecranus Perle et al., 1993. The list of characters offered below differs from that originally given by Perle et al. (1993, 1994), not only because some features exhibit a wider distribution than previously thought, but also since new features have been recognised. *Mononykus* differs from other alvarezsaurids in the following autapomorphies:

M1) Absence of pleurocoels in cervical vertebrae (Fig. 2). Presence of pleurocoels in cervical vertebrae is a common feature among Theropoda (Gauthier, 1986). This condition seems to be ancestral for the Alvarezsauridae, because pleurocoel openings are present in neck vertebrae of *Alvarezsaurus* (Bonaparte,

1991). Contrarily, cervical vertebrae of *Mononykus* lack pleurocoels (Perle et al., 1994), a character convergently acquired in ornithurine birds (Chiappe, in press).

M2) Presence of sulcus caroticus in cervical vertebrae (Fig. 2). In *Mononykus* the cranioventral margin of the cervical centra is complex, due to the presence of a craniocaudal groove laterally bounded by a strongly developed ventral processes. This ventral process of *Mononykus* resembles the processus caroticus of modern birds, in which the major muscle mass of *M. longus colli ventralis* is attached (Baumel & Witmer, 1993). This character is present in other

Mesozoic birds (e.g., *Ichthyornis*, *Hesperornis* and presumably *Patagopteryx*; Marsh, 1880; Alvarenga & Bonaparte, 1992), although it is unknown in other avialans (e.g., *Iberomesornis*, *Neuquenornis*; Sanz et al., 1988; Chiappe & Calvo, 1994). The phylogenetic status of this character is uncertain (i.e., synapomorphic of Metornithes or autapomorphic of *Mononykus*), mainly because the sulcus and lateroventral processes are absent in the cervicals of *Alvarezsaurus calvoi* (MUCPV 54).

M3) Presacral vertebrae with diapophyses and parapophyses occupying the same level (Fig. 5). Perle et al. (1994) noted this peculiar condition for *Mononykus* which is unique among Theropoda. The preserved dorsal vertebrae of *Patagonykus* (PVPH 37) show the ancestral archosaur condition in which the parapophyses are cranioventrally placed with respect to the diapophyses. The few dorsal vertebrae known in *Alvarezsaurus* correspond to the cranial region (Bonaparte, 1991).

M4) Dorsal vertebrae lacking hyposphene-hypantrum, and postzygapophyses lateroventrally oriented (Fig. 5). As Perle et al. (1994) described, all of the presacral vertebrae of *Mononykus* lack hyposphene-hypantrum articulations. However, these authors did not include this feature in the diagnosis of *Mononykus*, but interpreted it as an equivocal synapomorphy of Metornithes (Chiappe et al., this volume). However, I do not agree with this interpretation. Although it is true that *Mononykus* lacks hyposphenes (viz., the postzygapophyses are elongate and separated from each other by a deep cleft), the same is not true for *Patagonykus*, because the postzygapophyses are ventrally confluent in a block-like hyposphene, the proportions of which do not significantly differ from those of other theropods such as *Deinonychus* and *Allosaurus* (Ostrom, 1969; Madsen, 1976).

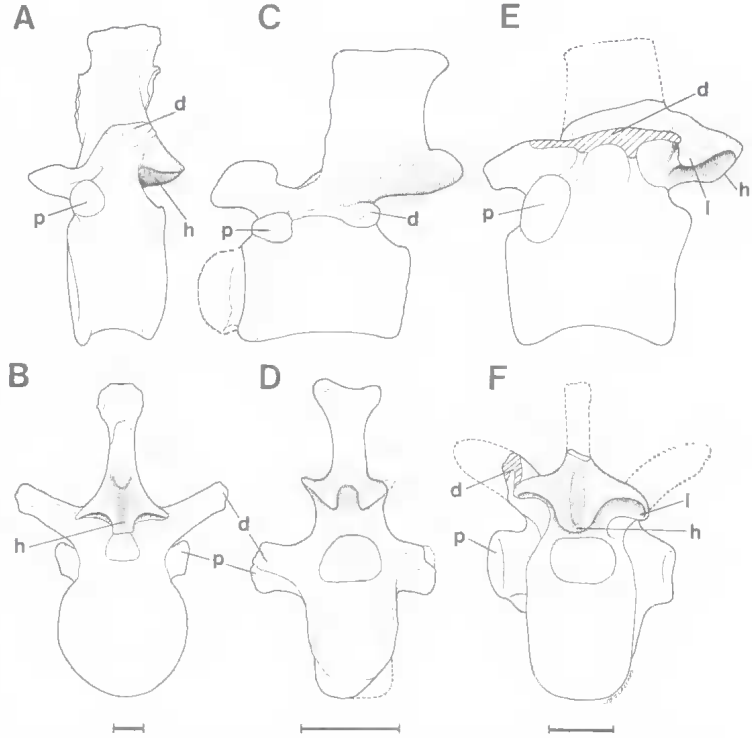


FIG. 5. Dorsal vertebrae of theropod taxa showing the morphology of the postzygapophyseal region. A, B, *Deinonychus antirrhopus* ('11th? dorsal vertebra'; from Ostrom, 1969). C, D, *Mononykus olecranus* ('middorsal'; modified from Perle et al., 1994). E, F, *Patagonykus puertai* (middorsal; PVPH 37). (A, C, E, left lateral; B, D, F caudal view). d=diapophysis, h=hyposphene, l=lateroventral margin of postzygapophysis, p=parapophysis; scale = 10mm.

Another curious aspect of *Mononykus* is that the articular surface of the postzygapophyses is flat and faces lateroventrally, a condition uniformly present along the dorsal series (Perle et al., 1994). On the contrary, the articular facet of the postzygapophyses in other theropods (e.g., *Allosaurus*, *Deinonychus*, *Patagonykus*) is ventrally concave and faces more ventrally than laterally.

M5) Cranial dorsal vertebrae transversally compressed. In *Mononykus* (Perle et al., 1994) the centra of the cranial dorsal vertebrae are strongly compressed transversely. As a result, a pronounced ventral keel is present in the cranial dorsal vertebrae. This condition is absent in the available dorsals of *Patagonykus* (PVPH 37), in which the centra are transversely wider and ventrally flat. Preserved cranial dorsal vertebrae of *Alvarezsaurus* (MUCPV 54) are transversely compressed and a slight ventral keel is present, but it is not so marked as in *Mononykus*.

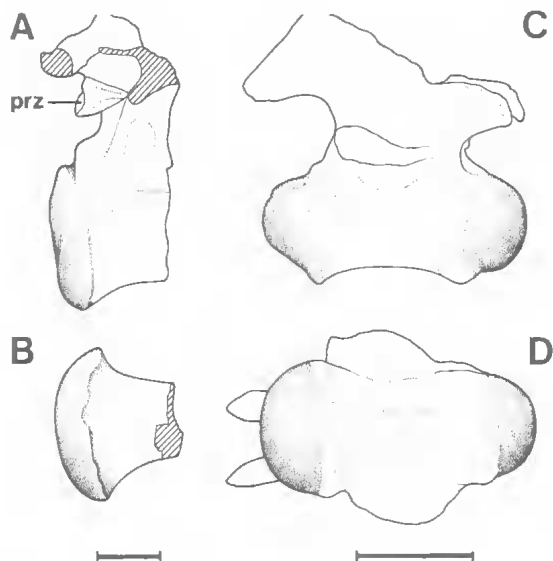


FIG. 6. Mids dorsal vertebrae of alvarezsaurids showing the morphology of central articular facets. A, B, caudal portion of dorsal vertebra of *Patagonykus puer tai* (PVPH 37). C, D, *Mononykus olecranus* (from Perle et al., 1994). (A, C, right lateral view; B, D, ventral; broken bone surface indicated by dashed lines). prz=prezygapophysis of another dorsal vertebra, adjacent caudally; scale = 10mm.

M6) Caudal dorsal vertebrae strongly procoelous. *Mononykus* is one of the few theropods in which caudal dorsal vertebrae are strongly procoelous. *Patagonykus* resembles *Mononykus* in that caudal dorsal vertebrae exhibit the procoelous condition, but they differ in that the convexity of the caudal articular surface of dorsal vertebrae is considerably more pronounced in *Mononykus* than in the Patagonian taxon (Fig. 6). In *Alvarezsaurus* the condition of the dorsal vertebrae is unknown. As Perle et al. (1993, 1994) pointed out, a strong procoelous condition for caudal dorsals is uncommon among theropods and the other case in which it was reported is the ornithothoracine bird *Patagopteryx* (Alvarenga & Bonaparte, 1992; Chiappe, 1992).

M7) Extreme transverse compression of the last sacral vertebra (Fig.7). The last sacral of *Mononykus* exhibits extreme transverse compression. This condition sharply differs from that present in *Patagonykus* and *Alvarezsaurus*, in which the sacral centra are considerably less compressed transversely. The transverse compression described for *Mononykus* is accompanied by a ventral projection of the centrum below the level of the caudal articular surface.

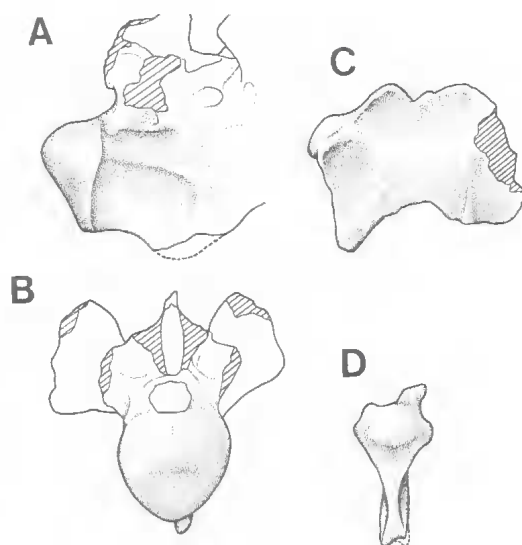


FIG. 7. Last sacral vertebrae of alvarezsaurids. A, B, *Patagonykus puer tai* (PVPH 37). C, D, *Mononykus olecranus* (GI N107/6 cast). (A, C, right lateral view; B, D, caudal). Scale = 10mm.

This modification is evident when the last sacral of both *Mononykus* and *Patagonykus* is compared in caudal aspect (Fig.7). In the first taxon the ventral keel nearly equals the dorsoventral depth of the caudal articular surface of the centrum, while in *Patagonykus* the ventral keel is considerably less developed with respect to the caudal articular surface. *Alvarezsaurus* shows the same condition as *Patagonykus*.

M8) Coracoidal shaft elliptical in lateral view (Fig. 3). The coracoid of *Mononykus* is elliptical, as seen in lateral aspect, being craniocaudally long and dorsoventrally low. This morphology is in sharp contrast to that of other maniraptorans (e.g., *Deinonychus*, *Sinornithoides*, *Archaeopteryx*, Ornithothoraces; Ostrom, 1969, 1974, 1976a; Russell & Dong, 1993; Walker 1981; Chiappe, 1996) in which the coracoid is dorsoventrally deeper than craniocaudally long with a rectangular to strut-like shape. The coracoid of *Mononykus* resembles the ancestral theropod condition (Gauthier, 1986), and is better interpreted as an evolutionary reversal that is diagnostic for this taxon. The actual shape of the coracoids of *Patagonykus* and *Alvarezsaurus* is not known (the reconstruction given in Fig. 3 is approximate). Hence, the distribution of this character may be wider than thought and its phylogenetic status different.

M9) Coracoid transversely flat (Fig.3). In *Mononykus* (GI N107/6) the lateral surface of the coracoid is slightly convex craniocaudally, but it is lateromedially flat. Instead, in *Patagonykus*, as well as other theropods (e.g., *Allosaurus*, *Deinonychus*, *Archaeopteryx*), the coracoid is strongly inflected medially, with the lateral surface proximodistally and craniocaudally convex. Also, *Patagonykus* has a sharp craniocaudal ridge along the lateral surface of the coracoid. Unfortunately, the coracoid of *Alvarezsaurus* is too poorly preserved to discern the condition of this feature.

M10) Sternum with thick carina. The presence of an ossified sternal keel is interpreted as a synapomorphy of Metornithes (Perle et al., 1993, 1994; Chiappe et al., this volume). *Mononykus*, however, is peculiar among avialians in that the sternal carina is transversely thick and V-shaped in cranial view, instead of being transversely narrow and T-shaped as in ornithothoracine birds (Perle et al., 1994, Chiappe et al., this volume). Unfortunately, the sternum is unknown in both *Alvarezsaurus* and *Patagonykus* and for this reason the condition described above for *Mononykus* constitutes an ambiguous autapomorphy of the later taxon.

M11) Radius with extensive articular surface for the ulna (Fig. 8). In *Mononykus* (Perle et al., 1994) the proximocaudal portion of the radius forms a single, extensive surface for articulation with the ulna. In *Patagonykus*, instead, two proximocaudal surfaces for the ulnar articulation are present. However, these surfaces are considerably smaller than those of the Mongolian taxon.

M12) Radius with carpal articular facet hypertrophied (Fig. 8). *Mononykus* is unique among theropods in the unusual development of the

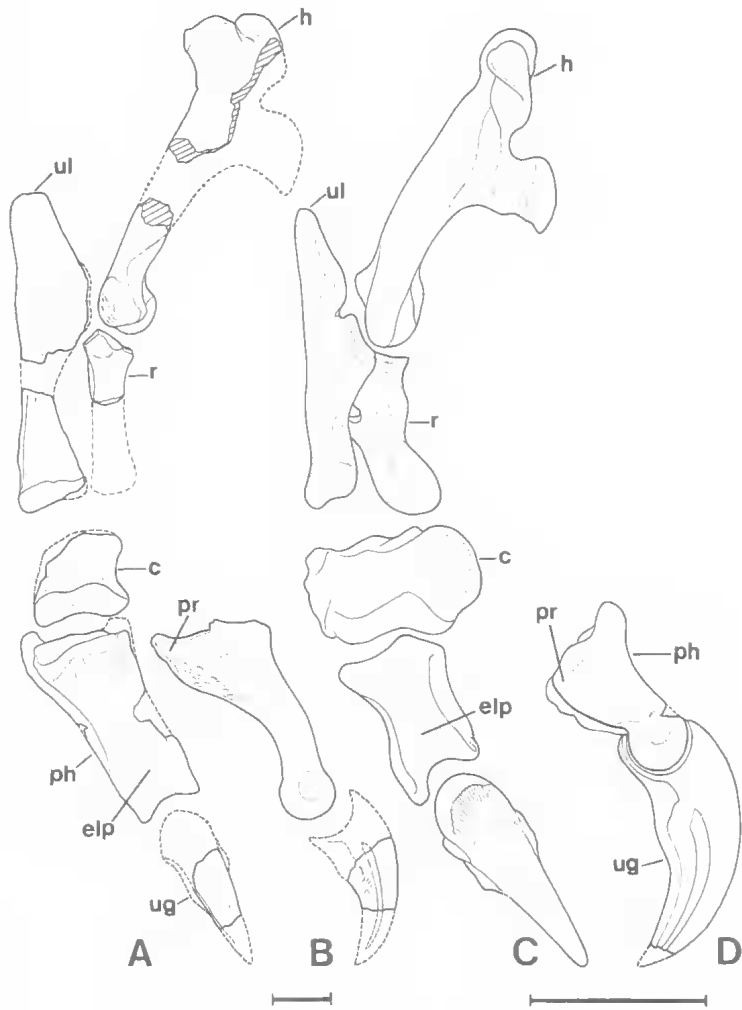


FIG. 8. Forelimbs of alvarezsaurids. A, B, composite reconstruction based on left and right forelimb bones of *Patagonykus puertai* (PVPH 37). C, D, *Mononykus olecranus* (from Perle et al., 1994). (A, C, lateral view; B, D, caudal view of first phalanx and unguis of digit I). c=carpometacarpus, elp=extensor ligamentary pit, h=humerus, ph=first phalanx, pr=proximo-medial ridge, r=radius, ul=ulna, ug=unguis; scale = 20mm.

radiocarpal articular facet (Perle et al., 1994). This morphology is almost certainly absent in *Patagonykus*, because the shaft of the radius is rod-like and triangular in cross section, lacking indications of the presence of an hypertrophied radiocarpal articular facet.

M13) First phalanx of digit I with a very prominent proximocaudal process (Fig. 8). In *Mononykus* the proximocaudal corner of the first phalanx of digit I develops a prominence that wraps over the ginglymus of metacarpal I. This

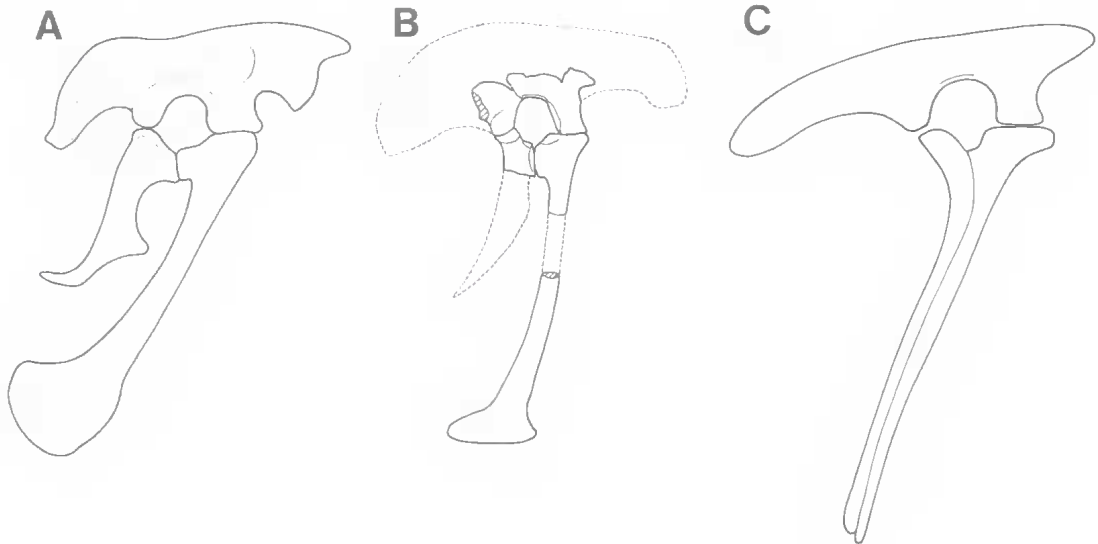


FIG. 9. Pelves of maniraptorans in lateral aspect. A, *Adasaurus mongoliensis* (from Barsbold, 1983). B, *Patagonykus puertai* (composite reconstruction based on left and right bones of the pelvis of PVPH 37). C, *Mononykus olecranus* (from Perle et al., 1994). Not to scale.

process, probably related to the insertion of strong extensor muscles, is absent in other theropods, including *Patagonykus*.

M14) Pubis caudoventrally oriented (Fig. 9). In *Mononykus* (Perle et al., 1994; Chiappe et al., this volume) the main axis of the pubic shaft describes an angle of nearly 70° with the proximal iliac surface of the pubis. In *Patagonykus*, instead, the proximal portion of the pubic shaft is oriented almost perpendicularly with respect to this surface of the pubis. The differences in pubic retroversion documented within Alvarezsauridae supports the interpretation that a strong caudoventral orientation of the pubis, becoming parallel to the ischium, evolved more than once within Metornithes: once in *Mononykus* and again in birds more derived than *Archaeopteryx* (Wellnhofer, 1974; 1988; 1993).

M15) Pubic foot absent (Fig. 9). *Mononykus* lacks a distal pubic foot (Perle et al., 1993, 1994; Chiappe et al., this volume). This feature was originally thought to be an ambiguous synapomorphy of Metornithes, because a distal foot was present in the basal ornithothoracine *Sinornis* (Sereno & Rao, 1992; Perle et al., 1993; Chiappe, 1995c). However, the absence of a distal foot in the pubis of *Mononykus* is interpreted as autapomorphic of this taxon, because a well developed distal expansion is documented in the pubis of *Patagonykus* and basal ornithothoracine birds. The pubes are not preserved in *Alvarez-*

saurus nor in the basal ornithothoracine bird *Iberomesornis* (Sanz et al., 1989). In the context of all the evidence, I interpret the lack of a pubic foot as independently evolved in *Mononykus* and ornithothoracines more derived than *Patagopteryx*.

M16) Ischium extremely reduced (Fig. 9). In *Mononykus* (Perle et al., 1993, 1994; Chiappe et al., this volume) the ischium is markedly reduced. In *Patagonykus* the ischium is also reduced with respect to other theropods (e.g., Ornithomimidae), but its proximal end, at least, is more massive than that of *Mononykus*. *Patagonykus* retained a well defined ischiac pedicle on the ilium, with the antitrochanter extending over both ilium and ischium. The articulation between pubis and ischium is dorsoventrally deep in the Patagonian taxon. In *Mononykus* the ilium and ischium are strongly fused, and the antitrochanter is formed by both pelvic bones (Perle et al., 1994).

M17) Femoral distal condyles transversely expanded, nearly confluent below popliteal fossa (Fig. 10). In *Mononykus* (Perle et al., 1994) the medial condyle of the femur is extremely expanded transversely, its transverse axis being nearly 75% of its craniocaudal extension. Perle et al. (1993, 1994) noted the distal enclosure of the popliteal fossa resembling the condition present in more derived birds (Chiappe & Calvo, 1994; Chiappe, 1992, 1995a). This enclosure of the popliteal fossa results from the transverse expan-

sion of both the medial distal condyle and the ectocondylar tuber, which are almost in contact with each other, distal to the popliteal fossa. On the contrary, in *Patagonykus*, as in other non-avian theropods (e.g., *Deinonychus*, Ornithomimidae, Tyrannosauridae) this fossa is entirely open distally, because both the medial condyle and the ectocondylar tuber are less expanded transversely. The modification described above for the femur of *Mononykus* correlates with that present in the proximal tibia, in which the outer condyle greatly expands transversely, contacting with the inner condyle of the same bone. In regard to the tibia, *Patagonykus* exhibits the ancestral condition, with the outer condyle less expanded transversely.

M18) Tibia with accessory (medial) cnemial crest. As interpreted by Perle et al. (1993, 1994), the presence of a smooth crest on the medial face of the proximal tibia is convergent with Ornithurae, because a medial crest is absent in Maniraptora ancestrally (e.g., *Deinonychus*; Ostrom, 1969), as well as in *Patagonykus*.

M19) Outer malleolus of distal tibia craniocaudally thick (Fig. 11). In *Alvarezsaurus* and *Patagonykus* the outer malleolus of the distal tibia is craniocaudally narrow with respect to that portion of the calcaneum that is in front of it, representing nearly 36% of the craniocaudal diameter of the calcaneum. In *Mononykus*, instead, the outer malleolus is craniocaudally thicker, representing nearly 143% of the craniocaudal dimension of that portion of the calcaneum that is in front of it.

M20) Astragalocalcaneum with deep intercondylar groove (Fig. 11). In *Mononykus* the fusion between astragalus and calcaneum is stronger, and the intercondylar groove deeper, than in both *Patagonykus* and *Alvarezsaurus*. In the latter two taxa the astragalocalcaneal suture is still visible.

M21) Ascending process of astragalus laterally displaced (Fig. 11). In *Mononykus* the ascending astragalar process is deeply notched along its medial margin, resulting in an ascending process transversely narrow in cranial view (Perle et al., 1994). Also, the ascending process of the astragalus appears to be more laterally placed than in other maniraptorans (e.g., *Patagonykus*, *Alvarezsaurus*, *Deinonychus*), as suggested by the overlap of the lateral margin of this process with the lateral margin of the tibia. This condition contrasts with that present in other Coelurosauria (e.g., Tyrannosauridae, Ornithomimidae, Dromaeosauridae, *Patagonykus*, *Alvarezsaurus*) in which the ascending process of the astragalus

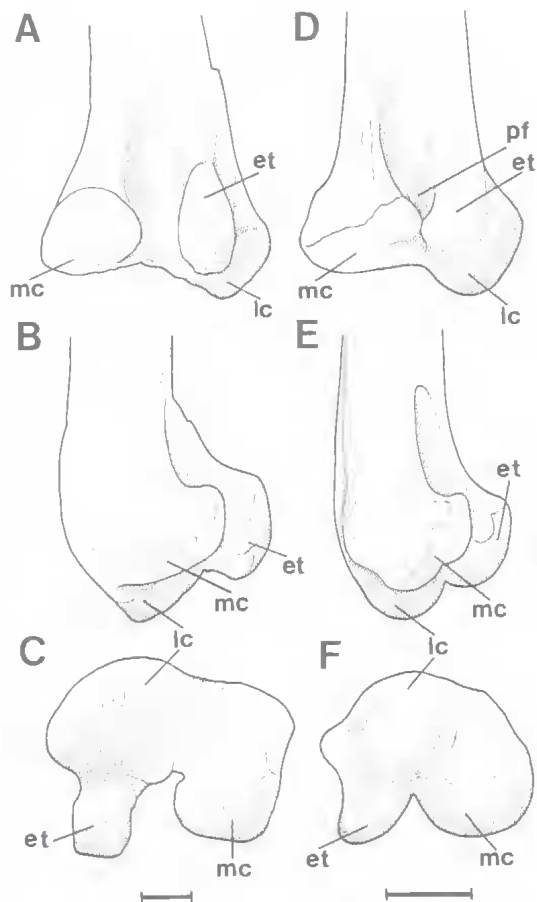


FIG. 10. Left distal femora of alvarezsaurids. A, B, C, *Patagonykus pueritai* (PVPH 37). D, E, F, *Mononykus olecranus* (from Perle et al., 1994). (A, D, caudal view; B, E, medial; C, F, distal). et=ectocondylar tuber, lc=lateral condyle, mc=medial condyle, pf=popliteal fossa; scale = 20mm.

is transversely wide. Particularly the medial margin of this process is not notched as in *Mononykus*, but extends in a nearly straight line from the medial condyle of the astragalus to the proximal tip of the ascending process. The lateral margin of the ascending process does not reach the lateral border of the tibia. Interestingly, the condition of *Mononykus* resembles that of modern avians, in which the 'pretibial bone' (homologous to the ascending process of the astragalus; McGowan, 1985) is transversely narrow and laterally displaced.

M22) Femoral trochanteric crest present. In Coelurosauria ancestrally (e.g., Ornithomimidae, Tyrannosauridae), as well as in *Deinonychus* (MCZ 4371), *Patagonykus*, *Alvarezsaurus* and

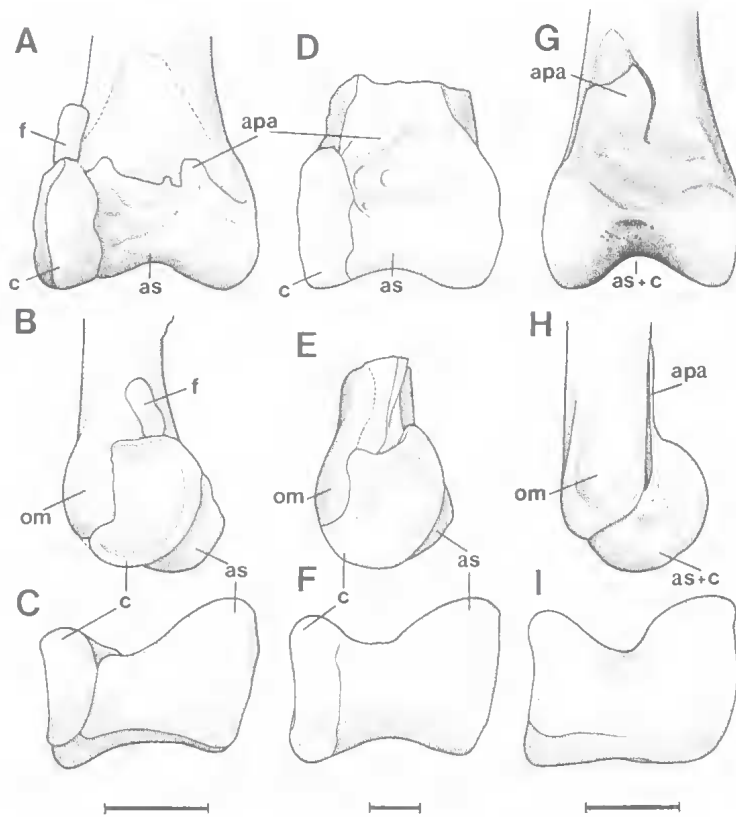


FIG. 11. Right distal tibia and astragalocalcaneum of Alvarezsauridac. A, B, C, *Alvarezsaurus calvoi* (MUCPV 54). D, E, F, *Patagonykus puertai* (PVPH 37). G, H, I, *Mononykus olecranus* (GI N107/6). (A, D, G, cranial view; B, E, H, lateral; C, F, I, distal; reconstruction indicated by dashed lines). as=astragalus, apa=ascending process of astragalus, c=calcaneum, f=fibula, om=out tibial malleolus; scale = 10mm.

Archaeopteryx, both anterior and greater femoral trochanters are separated by a cleft. In contrast *Mononykus* exhibits a femoral trochanteric crest (e.g., anterior trochanter undivided from the greater trochanter), a derived condition that is shared with more derived birds.

M23) Fibula does not articulate with the tarsus (Fig. 11). This feature was originally considered by Perle et al. (1993) as synapomorphic of Metornithes, because it is shared by *Mononykus* and the Ornithothoraces. However, other alvarezsaurids exhibit the plesiomorphic condition: in *Patagonykus* the fibula is incomplete, but the presence of a deep socket on the proximal calcaneal surface suggests that in this taxon the fibula articulated with the tarsus, a condition that also found in *Alvarezsaurus* (Bonaparte, 1991).

INGROUP RELATIONSHIPS. *Patagonykus* and *Mononykus* share seventeen characters which are absent or unknown in *Alvarezsaurus*. The monophyly of Alvarezsauridae is supported here by eleven derived characters.

Patagonykus + *Mononykus* clade. Several features support the conclusion that *Patagonykus* and *Mononykus* are more closely related than either is to *Alvarezsaurus*. Some of these features are absent in *Alvarezsaurus* and are readily interpreted as synapomorphic of the *Patagonykus* + *Mononykus* clade (characters 1 & 2), others are contingent upon the results of the cladistic analysis (characters 3 & 4). However, the condition of most of the apomorphies uniting *Patagonykus* and *Mononykus* is unknown for *Alvarezsaurus*, because of the fragmentary nature of the available material. Consequently, a large set of characters (5 through 17) used to unite *Patagonykus* + *Mononykus* may become synapomorphic of a more inclusive group (e.g., Alvarezsauridae), pending additional information on *Alvarezsaurus*:

1) Caudal articular surface of the centra of the last sacral and proximal caudal vertebrae strongly spherical. *Mononykus*, *Patagonykus* and *Alvarezsaurus* clearly differ from other theropods since they share last sacral and most of the caudal vertebrae with a ball-shaped caudal surface (character 19). However, *Alvarezsaurus* seems to be less derived than other alvarezsaurids because the caudal surfaces of the last sacral vertebra and caudal vertebrae are not as spherical as in *Patagonykus* and *Mononykus*. Moreover, the procoelous condition in *Alvarezsaurus* appears to be confined to the last sacral and to the caudal vertebrae, since the cranial articular surface of the presumed sacral 2 of *Alvarezsaurus* is almost planar.

2) Sacral vertebrae ventrally keeled (Fig. 7). In *Allosaurus* (Gilmore, 1920), *Gallimimus*

(Osmólska et al., 1972) and *Archaeornithomimus* (AMNH 6567) the ventral surface of sacral centra is smooth and convex in cross-section. This condition also applies to *Ornithomimus* (USNM 2164; see Gilmore, 1920), although in this taxon the sacral centra are ventrally grooved. The sacral centra of *Deinonychus* (MCZ 4371), *Ornitholestes* (AMNH 619) and *Archaeopteryx* (Wellnhofer, 1974, 1993) are not keeled ventrally. Sacral vertebrae are not keeled in *Iberomesornis* and *Sinornis* (Sanz et al., 1988; Chiappe, pers. comm.) and the same is true for more derived birds (e.g., *Ichthyornis*, *Hesperornis*; Marsh, 1880): other avialans, instead, bear a ventral groove (e.g., *Baptornis*, *Patagopteryx*; Martin & Tate, 1976; Chiappe, 1992; Perle et al., 1994). Alvarezsaurids differ from the remaining Coelurosauria in the presence of a ventral keel in the caudal sacral vertebrae. However, the degree of transverse compression of this keel varies among alvarezsaurids: in *Alvarezsaurus* (MUCPV 54) the presumed sacral 1 is transversely wide and ventrally convex in cross-section, while the sacrals 2-3 are ventrally grooved, resembling the condition present in *Ornithomimus* (Gilmore, 1920). The penultimate sacral vertebra of *Alvarezsaurus* (presumably sacral 4) is more compressed transversely than more cranial sacrals; this vertebra is slightly keeled, but a rudimentary ventral canal is still present. The last sacral (presumably sacral 5) of *Alvarezsaurus* bears a ventral keel, but it is not so prominent and transversely compressed as in *Patagonykus* and *Mononykus*. In *Patagonykus* (PVPH 37) the transverse compression of the ventral keel increases caudally, show-

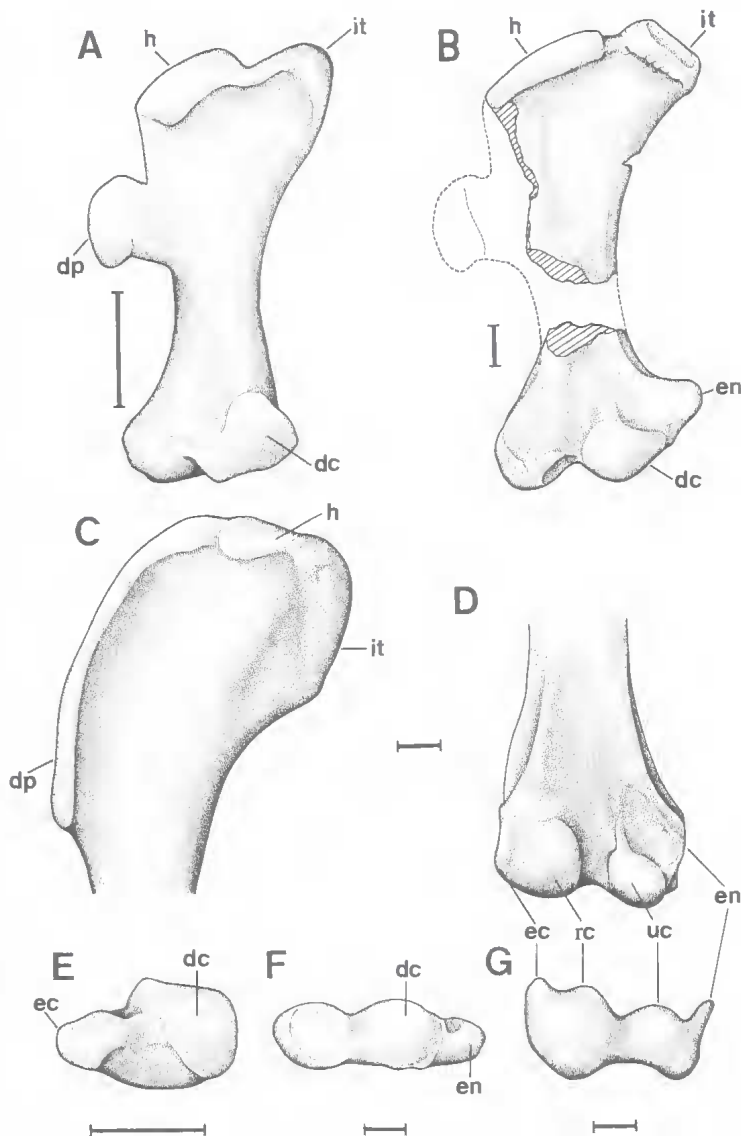


FIG. 12. Humeri of theropod taxa. A, E, *Mononykus olecranus* (modified from Perle et al., 1994). B, F, *Patagonykus puertai* (composite reconstruction based on left and right humerus of PVPH 37). C, D, G, *Deinonychus antirrhopus*; C, proximal end (from Ostrom, 1969), D, G, distal end of humerus (reconstruction based on AMNH 3015 and MCZ 4371). (A, B, C, D, cranial view; E, F, G, distal). dc=distal condyle, dp=deltopectoral crest, h=humeral head, ec=ectepicondyle, en=entepicondyle, it=internal tuberosity, rc=radial condyle, uc=ulnar condyle; scale = 10mm.

ing the maximum compression in the last sacral (presumably sacral 5). In *Mononykus* the first sacral is transversely more compressed than the dorsal vertebrae (Perle et al., 1994) and exhibits a slight longitudinal ridge along its ventral surface. I interpret *Mononykus* as more derived than

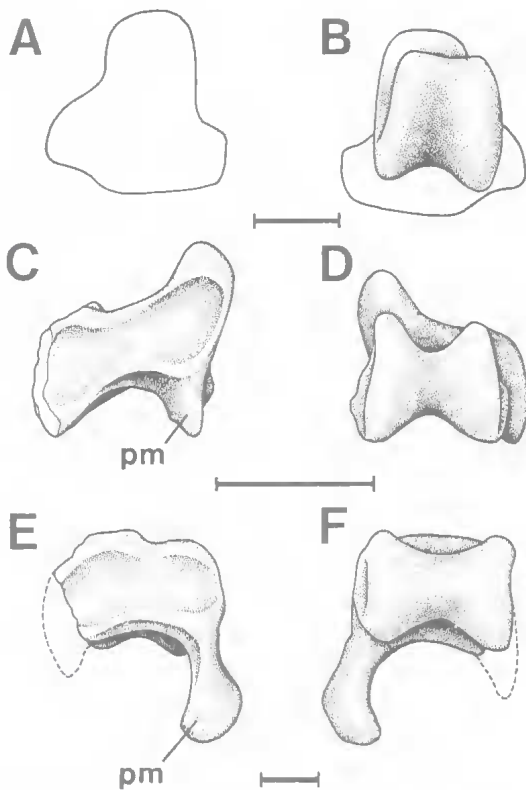


FIG. 13. First phalanx of digit I of maniraptoran theropods. A, B, *Deinonychus antirrhopus* phalanx of the left manus (A, taken from Ostrom, 1969; B, from YPM 5206). C, D, *Mononykus olecranus* phalanx of the right manus (C, from Perle et al., 1994; D, from GJ NI07/6). E, F, *Patagonykus puertai* phalanx of the right manus (PVPH 37). (A, C, E, proximal view; B, D, F, distal). pm=proximomedial ridge; scale = 10mm.

other alvarezsaurids in this respect, since the sacrals are extremely compressed laterally (Perle et al., 1994; see character M7).

3) Femoral fourth trochanter present. A femoral fourth trochanter is present in basal coelurosaurids (e.g., Ornithomimidae, Tyrannosauridae). This structure has been retained, albeit reduced, in dromaeosaurids as it is seen in *Deinonychus* (MCZ 4371; contra Ostrom, 1976b). *Archaeopteryx*, *Alvarezsaurus*, and Ornithothoraces lack the fourth trochanter, a condition interpreted as synapomorphic of Avialae. In the context of the evidence, the shared presence of a fourth trochanter in *Mononykus* and *Patagonykus* is considered as an apomorphic reversal.

4) Supracetabular crest present. The absence of a supracetabular crest is hypothesised as

synapomorphic of Maniraptora, because such a crest is lacking in *Deinonychus*, *Archaeopteryx*, *Alvarezsaurus* and the Ornithothoraces. Following that, the presence of such a crest in the ilium of *Patagonykus* and *Mononykus* is interpreted as a secondary reversal.

5) Posterior dorsal vertebrae procoelous (Fig. 6). *Patagonykus* and *Mononykus* share procoelous caudal dorsal vertebrae. However, in the first taxon the convexity of the caudal articular surface is considerably less marked than in *Mononykus*, in which this surface is ball-shaped. Interestingly, the development of a ball-shaped, caudal articular surface in sacral vertebrae is almost the same in *Patagonykus* and *Mononykus* (Fig. 7) suggesting that the procoelous condition evolved from caudal to dorsal vertebrae. Mid and caudal dorsal vertebrae are unknown in *Alvarezsaurus* (Bonaparte, 1991), but it is possible that they may have been amphiplatyan or amphicoelous, since the disarticulated second sacral vertebra of the holotype (MUCPV 54) has a flat caudal surface. *Alvarezsaurus*, however, is coded as a question mark for this character.

6) Bicipital tubercle of coracoid absent (Fig. 3). A bicipital tubercle is absent in the coracoids of *Mononykus*, *Patagonykus* and presumably also in *Alvarezsaurus* (unfortunately, most of the caudal and distal portions of the coracoid are missing in the holotype). This condition sharply contrasts with that present in Theropoda ancestrally. For example, in *Allosaurus* the bicipital tubercle is slightly marked, but it forms a distinct prominence on the lateral surface of the coracoid, as is seen in caudal view (Madsen, 1976). In ornithomimids (e.g., *Ornithomimus* AMNH 5355; *Archaeornithomimus* AMNH 6567, 6566) the biceps tubercle is also prominent, but it is even more developed in maniraptorans. Such is the case for *Deinonychus* (YPM 5236), which exhibits a biceps tubercle more developed than in most theropods (Ostrom, 1974) and *Archaeopteryx* in which the tubercle is proportionally larger than that of *Deinonychus* (Ostrom, 1974; Wellnhofer, 1988, 1993). In avialians more derived than *Archaeopteryx* (e.g., Enantiornithes; Walker, 1981) the acrocoracoid (hypothesised as the homologue of the bicipital tubercle; Ostrom, 1976a), consists of a robust structure, that in the Ornithothoraces is proximally placed with respect to the glenoid facet (Chiappe, 1992).

7) Forelimbs less than 20% of hindlimb length. In Theropoda ancestrally the forelimbs represent 40-53% of hindlimb length, as it occurs in

Herrerasaurus, *Coelophysis*, *Syntarsus*, *Dilophosaurus*, *Piatnitzkysaurus* and *Compsognathus* (Raath, 1969; Colbert, 1989; Ostrom, 1978; Welles, 1984; Novas, 1994; Sereno, 1994). Possession of extremely short forelimbs (with respect to hindlimb length) seems to have evolved more than once in theropod evolution (Novas, 1992; Perle et al., 1994). Examples of such shortening are seen in the neoceratosaurian theropods (e.g., *Ceratosaurus*, *Carnotaurus*; Bonaparte et al., 1990; Novas, 1992), the basal tetanurine *Torvosaurus* (Galton & Jensen, 1979; Holtz, 1994) and the coelurosaurian Tyrannosauridae (Novas, 1991, 1992; Holtz, 1994). In the latter taxon the forelimbs represent 22-26% of the hindlimb length (Lambe, 1917), but in *Mononykus* the forelimbs are even shorter than in tyrannosaurids, since they represent nearly 18% of the length of the hindlimbs (Perle et al., 1993, Fig. 2). In *Patagonykus* (PVPH 37) the forelimbs are known from portions of humerii, ulnae and the almost complete left manus (carpometacarpus plus digit I). Although it is not possible to obtain a ratio of forelimb versus hindlimb length for *Patagonykus*, the proportions of the currently available bones of this taxon suggest that the forelimbs also were very short. Bonaparte (1991) arrived at the conclusion that *Alvarezsaurus* possibly had reduced forelimbs on the basis of the proportionally reduced scapular girdle of this theropod. This suspicion is supported by the stout aspect and large size of the ungual phalanx of digit I (Fig. 4). The morphology of this ungual allows the prediction that the proximal elements of the forelimb of *Alvarezsaurus* were morphologically similar to those of *Mononykus* and *Patagonykus* (Perle et al., 1993, 1994).

8) Humeral head with major transverse axis ventrolaterally inclined with respect to the longitudinal axis of the humerus, and internal tuberosity proximally projected (Fig. 12). In *Mononykus* the humeral head is lateroventrally inclined with respect to the longitudinal axis of the humerus. Additionally, the internal tuberosity is proximally projected, reaching nearly the same level as the humeral head. By contrast, in other theropods (e.g., *Deinonychus*; Ostrom, 1969) the major transverse axis of the humeral head is horizontally held with respect to the longitudinal axis of the humerus, or it is inclined ventromedially (e.g., *Ichthyornis*; Marsh, 1880) with respect to the longitudinal axis. Also, in most theropods the internal tuberosity is a cone-shaped structure (e.g., Ceratosauria, Tyrannosauridae, *Ornitholestes* AMNH 619; Rowe & Gauthier,

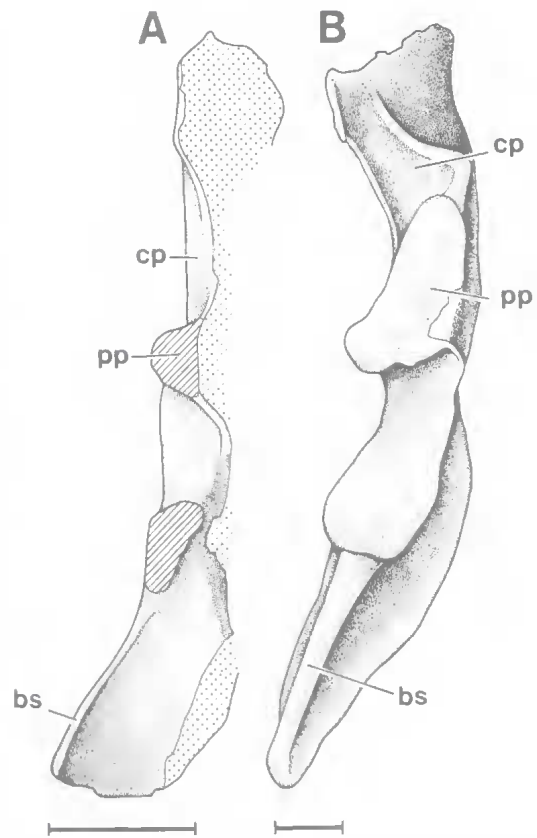


FIG. 14. Ilium of maniraptoran theropods in ventral aspect. A, right ilium of *Alvarezsaurus calvoi* (MUCPV 54). B, left ilium (reversed) of *Deinonychus antirrhopus* (AMNH 3015). Sandstone matrix indicated by stippling. bs=brevis shelf, cp=fossa for origin of *M. cuppedicus*, pp=pubic peduncle; scale = 20mm.

1990; Osborn, 1917), or it forms a longitudinally expanded prominence that is medially and slightly caudally projected, and distally placed with respect to the humeral head (e.g., *Deinonychus*, *Ichthyornis*; Marsh, 1880; Ostrom, 1969). The known humerus of *Patagonykus* has unconnected proximal and distal portions, such that determination of the orientation of the humeral head and internal tuberosity with respect to the humeral shaft is difficult to assert. However, the proximal end of the humerus of *Patagonykus* closely resembles that of *Mononykus*, and the features described above for the later taxon seem to apply also to the Patagonian species. Since the humerus is unknown in *Alvarezsaurus* (Bonaparte, 1991) the peculiar morphology of the proximal end of the humerus shared by *Patagonykus* and

Mononykus is considered as an ambiguous synapomorphy of the Alvarezsauridae.

9) Humerus with a single distal condyle; ulna and radius tightly appressed proximally, forming a cup-like articular surface for the humerus (Fig. 12). In Theropoda, ancestrally (for example, *Piatnitzkysaurus* MACN-CH 895; *Deinonychus* AMNH 3015, MCZ 4371; *Ornitholestes* AMNH 619; Ornithomimidae; Barsbold & Osmólska, 1990), the distal end of the humerus exhibits two distal condyles, the radial one being larger than the ulnar condyle. Both ulnar and radial condyles are separated by an intercondylar groove, a condition that is retained in recent birds (Baumel & Witmer, 1993). Also, the humeral cotylus of the ulna is subtriangular in proximal view, with an acute cranial projection and a craniolateral concavity for the reception of the radius. In Theropoda, ancestrally, the radius and ulna lack proximal articular facets between them. Also, the ulna and radius bear independent proximal articular surfaces for the ulnar and radial condyles of the humerus, respectively. Alvarezsaurids, instead, are unique among archosaurs in the peculiar propodial-epipodial articulation, consisting in the presence of a single, and well developed, condyle in the distal humerus which articulates with a continuous, cup-like articular surface formed by both radius and ulna. In *Patagonykus* and *Mononykus* the humeral cotylus of the ulna is subelliptically shaped and lacks the lateral concavity to accommodate the radius. The latter bone has moved entirely over the cranial aspect of the ulna and both bones are tightly articulated proximally.

Some minor differences exist in the propodial-epipodial articulation of alvarezsaurids (Fig. 12): while in *Patagonykus* the humeral distal condyle is ball-shaped and elliptical in contour, in *Mononykus* it is trochlear and trapezoidal in distal aspect. The complex morphology of the distal humeral condyle of *Mononykus* is due to the strong craniocaudal expansion of its medial side, equalling its transverse axis (Fig. 12A, E). Furthermore, the proximal articulation between the radius and ulna is extremely extended in *Mononykus* (Perle et al., 1994) and is readily interpreted as autapomorphic for the Mongolian taxon (see character M11).

10) Olecranal process of ulna strongly developed (Fig. 8). The development of the olecranal process is variable within Dinosauria, although it is feebly developed in most theropods (e.g., *Syntarsus*, *Piatnitzkysaurus*, *Allosaurus*, Ornithomimidae, *Deinonychus*, *Archaeopteryx*,

Ornithothoraces; Ostrom, 1969, 1976a; Raath, 1969; Madsen, 1976; Bonaparte, 1986a; Baumel & Witmer, 1993; Barsbold & Osmólska, 1990). *Patagonykus* and *Mononykus* differ from the remaining dinosaurs because they share a strongly developed ulnar olecranon process: that in *Mononykus* represents 40% of the whole length of the bone (Perle et al., 1994). The relative size and the stout morphology of the ungual phalanx of manual digit I of *Alvarezsaurus* (see characters 7 & A5) suggests that the presence of a well developed olecranal process probably had a distribution wider than thought.

11) Ulnar caudal margin straight (Fig. 8). Gauthier (1986) considered '*ulna bowed posteriorly*' as a diagnostic character of Maniraptora. Avialae and *Deinonychus*, and apparently also in *Troodon* and *Sinornithoides* (Russell, 1969; Russell & Dong, 1993b) the caudal border of the ulna is uniformly convex, excepting the distal extremity that, as in other tetanurines, is posteriorly projected (the ulna is slightly bowed in the Ornithomimidae, although it is not convex caudally but cranially — that is towards the radius; Nicholls & Russell, 1985; Barsbold & Osmólska, 1990; Osmólska et al., 1972). In *Mononykus* (Perle et al., 1994) the ulna is straight in lateral and cranial aspects. Preserved portions of the ulna of *Patagonykus* show that the caudal margin is straight. The straight shaft of the ulna in alvarezsaurids is interpreted as an evolutionary reversal that might be related to the strong reduction of the forelimbs.

12) Carpometacarpus massive, short and quadrangular (Fig. 8). *Patagonykus* and *Mononykus* share a carpometacarpus (= semilunate carpal + first metacarpal) that is dorsoventrally compressed and quadrangular in dorsal view, a condition quite unusual for a theropod (Perle et al. 1994; Novas, in press a). In *Patagonykus* and *Mononykus* the distal condyle of metacarpal I is transversely wide and dorsoventrally compressed, with a shallow dorsoventral groove. In contrast to other theropods such as *Herrerasaurus* (PVSJ 373; Sereno, 1994), *Coelophysus* (Raath, 1969), *Torvosaurus* (Galton & Jensen, 1979), *Allosaurus* (Madsen, 1976) and *Deinonychus* (Ostrom, 1969), metacarpal I is proximodistally long and transversely narrow and the distal end forms a ginglymoid articulation. *Mononykus*, and presumably also *Patagonykus*, differ from other coelurosaurids (e.g., *Oviraptor*, *Deinonychus*, *Velociraptor*, *Archaeopteryx*; Ostrom, 1976a; Barsbold et al., 1990) in that the semilunate carpal articulates

distally only with metacarpal I, instead of with both metacarpal I and II as in Maniraptora ancestrally (Gauthier, 1986). Size disparity between metacarpal I and the semilunate carpal is readily apparent in alvarezsaurids: the transverse width of metacarpal I nearly matches that of the semilunate carpal. This disparity is probably due to hypertrophy of the metacarpal I.

The main difference between *Mononykus* and *Patagonykus* is that in the first taxon the semilunate articulation of the carpometacarpus is considerably more extended cranially and distally than in *Patagonykus*, resulting in a very close approximation between the semilunate articulation and the distal condyle of the metacarpal I. In *Deinonychus* and *Archaeopteryx* (Ostrom, 1969, 1976a) the medial (cranial, if rotated) margin of the metacarpal I forms a narrow ridge, resembling the condition described for *Mononykus* (Perle et al., 1994).

13) Digit I larger than the remaining digits of the hands (Fig. 8). The hand of most coelurosaurs is characterised by being gracile and elongate, with the first digit smaller than the second digit, both in length and in transverse diameter (Ostrom, 1969; Gauthier, 1986; Barsbold et al., 1990). In *Mononykus*, instead, digit I is much larger (in both transverse width and proximodistal length) than digits II and III. As noted by Perle et al. (1994), metacarpals II and III are not only strongly reduced, but they are fused to each other and with metacarpal I, without the delimitation of any intermetacarpal space. Interestingly, the oviraptorosaur *Ingenia* (Barsbold et al., 1990) constitutes the only known non-alvarezsaurid theropod in which digit I is proportionally larger than the outer digits, although the degree of the reduction of the external digits is not so marked as in *Mononykus*. Close resemblances of the available manual bones of *Patagonykus* and *Alvarezsaurus* suggest that the South American taxa also shared the condition described above for *Mononykus*.

14) Phalanx I of manual digit I showing B-shaped proximal articular surface, hook-like proximomedial processes, symmetrical distal ginglymus and deep extensor ligamentary pit (Fig. 13). *Patagonykus* and *Mononykus* are unique among Archosauria in the morphology of the first phalanx of digit I. This phalanx is craniocaudally wide and lateromedially compressed, resulting in a curious proximal articulation, which describes a horizontal 'B' in proximal aspect. This morphology sharply contrasts with that seen in other theropods, in which the

proximal contour of the first phalanx of digit I is triangular (e.g., *Deinonychus*; Ostrom, 1969), or describes a vertical rectangle (as in *Allosaurus*; Madsen, 1976). Another peculiarity is the presence of a pair of strongly developed proximomedial ridges bearing muscle scars. Distally, the ginglymus of the first phalanx forms a craniocaudally wide, symmetrical pulley, proximally preceded by a deep extensor ligamentary pit (Figs 8 & 13). By contrast, in other dinosaurs (e.g., *Mussaurus* MLP 68-II-27-1; *Deinonychus* YPM 5206; *Allosaurus*; Madsen, 1976), the ginglymus is transversely more compressed and the extensor pit is absent. Further, the flexor ligamentary pit is more marked in *Mononykus* and *Patagonykus* than in other theropods.

15) Medial condyle of femur transversely wide and distally flat (Fig. 10). The medial condyle of the distal femur is transversely narrow and distally convex in non-avian theropods (e.g., *Allosaurus* CM 21726; *Tyrannosaurus* CM 9380; *Deinonychus* MCZ 4371), *Archaeopteryx* (Eichstatt specimen, cast) and early Ornithothoraces (e.g., *Enantiornithes*, MACN unnumbered cast). In *Patagonykus* and *Mononykus*, instead, the medial condyle of the distal femur is rectangular and distally flat. In the Patagonian taxon the transverse axis of this condyle represents nearly 66% of its craniocaudal extension, while in *Mononykus* it is 75%. The transverse extension of the medial condyle of the distal femur resembles that present in recent birds, such as *Rhea* (pers. collection).

16) Ectocondylar tuber caudally projected, well behind the medial distal condyle (Fig. 10). In *Allosaurus* (Gilmore, 1920), *Ornitholestes* (AMNH 619), *Gallimimus* (Osmólska et al., 1972), *Tyrannosaurus* (USNM 10.754) and *Deinonychus* (MCZ 4371), the ectocondylar crest of the femur does not caudally surpass the level of the medial femoral condyle. In *Patagonykus* and *Mononykus*, instead, the ectocondylar crest strongly projects caudally, surpassing the medial femoral condyle. This condition resembles that present in modern birds (e.g., *Rhea*) in which the crista tibiofibularis (the caudal portion of which is considered to be homologous with the ectocondylar tuber; Chiappe, 1996) is more caudally projected than the medial condyle of the femur.

17) Fibular condyle of femur conical and projected distally (Fig. 10). In *Mononykus* and *Patagonykus* the fibular condyle of the femur constitutes a well defined, cone-shaped structure, which is strongly projected distally. This condi-

tion contrasts with that seen in other theropods (e.g., *Allosaurus*; *Archaeornithomimus*, AMNH 6570; *Deinonychus*) in which the lateral condyle of distal femur is only slightly more projected distally with respect to the medial condyle. The lateral condyle of the femur is conical in some ornithomimids (e.g., *Gallimimus*, Osmólska et al., 1972, pl. 46), as well as in the tyrannosaurid *Alectrosaurus* (AMNH 6554), but in neither case is it so prominent as in alvarezsaurids. The condition of this femoral condyle in *Archaeopteryx*, *Iberomesornis* and the enantiornithine *Sinornis* is unknown (Ostrom, 1976a; Wellnhofer, 1974; Sanz et al., 1988; Sereno & Rao, 1991, Chiappe, 1995c), but in more derived avialians (e.g., *Hesperornis*, *Ichthyornis*, *Patagopteryx*, Enantiornithes; Marsh, 1880; Walker, 1981; Alvarenga & Bonaparte, 1992) the fibular condyle of femur is not conical but smoothly convex craniocaudally and transversely.

Alvarezsauridae Bonaparte, 1991. Alvarezsauridae is here defined to encompass *Patagonykus puertai*, *Alvarezsaurus calvoi*, *Mononykus olecranus* and all the descendants of their most recent common ancestor. Alvarezsauridae is diagnosed on the basis of nine unambiguous synapomorphies, plus other two ambiguous traits, which are listed and analyzed below:

18) Cervical vertebrae with craniocaudally short and dorsoventrally low neural spines (Fig. 2). *Alvarezsaurus* and *Mononykus* exhibit strongly reduced neural spines on the cervical vertebrae (Bonaparte, 1991; Perle et al., 1994). This condition strongly differs from those in other coelurosaurs. As an example, in *Ornitholestes* (AMNH 619) the neural spine of cervical ?4 is dorsoventrally deep and craniocaudally short, similar to *Deinonychus* (Ostrom, 1969). The neural spine of a mid-caudal cervical of *Ornitholestes*, instead, is dorsoventrally low but axially long. In *Archaeopteryx*, cervicals 4 and 5 (Wellnhofer, 1974) exhibit neural spines proportionally taller than *Mononykus* (Perle et al., 1994) and *Alvarezsaurus* (Bonaparte, 1991). Unfortunately, the neck vertebrae of basal avialians is almost unknown (e.g., *Iberomesornis*, *Sinornis*; Sereno & Rao, 1992) and the condition is unknown in *Patagonykus*. As originally noted by Bonaparte (1991), gracile cervical vertebrae with reduced neural spines are present in ornithomimids, a condition that is here interpreted as independently evolved.

19) Sacral and caudal vertebrae procoelous (Fig. 7). In Theropoda ancestrally the sacral and

caudal vertebrae are amphiplatyan or slightly amphicoelous (e.g., *Piatnitzkysaurus* MACN-CH 895; *Archaeornithomimus* AMNH 6567; *Albertosaurus* AMNH 5458; *Deinonychus* MCZ 4371). In the recently described seventh specimen of *Archaeopteryx* (Wellnhofer, 1993), the disarticulated and well preserved proximal caudals appear to be amphiplatyan, as suggested by the straight cranial and caudal margins of the caudal centra, parallel to each other in lateral view. The condition is unknown in basal Ornithothoraces (e.g., *Iberomesornis*; Sanz et al., 1988) due to the firm articulation among caudal segments forming a pygostyle. A procoelous condition of caudal dorsals, sacrals and caudals has been documented only in *Patagopteryx* among ornithothoracines (Chiappe, 1992, 1995a), a condition that was previously interpreted as convergently acquired with Alvarezsauridae (Perle et al., 1993, 1994). In Hesperornithiformes, ancestrally (e.g., *Baptornis*; Martin & Tate, 1976), the caudal centra are amphicoelous or amphiplatyan. In *Ichthyornis* (Marsh, 1880) the cranial surface of the first sacral centrum and the caudal surface of the last sacral vertebra are concave and the caudal vertebrae are amphicoelous.

Mononykus, *Patagonykus* and *Alvarezsaurus* exhibit the last sacral and most of the caudal vertebrae with a ball-shaped caudal surface. As commented above (character 1) some variation exists in the convexity of the caudal surface within Alvarezsauridae.

The resemblances between the proximal caudals of *Patagonykus* and eusuchian crocodyles (e.g., *Caiman*; pers. collection) are noteworthy, mainly because they share ball-shaped caudal articular surfaces, robust, craniocaudally short neural spines, transversely thin ligamentary scars at the base of the neural spines, and the base of the neural spines with a deep excavation between pre- and postzygapophyses. It is not possible to assert whether these osteological resemblances between *Patagonykus* and extant crocodyles correspond with similarities in distribution and development of the epaxial musculature, but the existence of a strong procoelous condition suggests a high degree of movement all along the tail, in contrast with most tetanurine theropods, including birds (Gauthier, 1986).

20) Caudal sacral centra transversely compressed. As noted above (character 2) the sacral vertebrae of alvarezsaurids are transversely compressed, in contrast with other theropods in which the sacrum does not exhibit such a condition.

21) Haemal arches of proximal caudals dorsoventrally elongate. This feature was interpreted by Martin & Rinaldi (1994) in support of non-avian affinities of *Mononykus*. However, in the context of all the evidence, the presence of elongate haemal arches in *Mononykus* and *Alvarezsaurus* is interpreted here as an apomorphic reversal, and consequently as diagnostic of the Alvarezsauridae.

22) Ungual phalanx of manual digit I stout and robust (Figs 4 & 8). Perle et al. (1993, 1994) have noted that the unguis of digit I of *Mononykus* is robust and less arched than in other theropods (e.g., *Deinonychus*, *Archaeopteryx*) and with the proximoventral area forming a flat surface lacking a flexor tubercle. These authors have indicated also, that the unguis of the first digit represents 226% of the proximodistal length of the carpometacarpus (Perle et al., 1994). As commented above, the manual unguis of *Alvarezsaurus* is remarkably similar to that of *Mononykus*, in being quadrangular in proximal aspect, with the proximoventral surface flat and the flexor tubercle absent. This manual unguis, outstandingly larger than any unguis of the foot, exhibits deep proximal concavities for articulation with the first phalanx of digit I. These concavities are separated by a prominent ridge. The unguis of digit I of *Alvarezsaurus* lacks the foramina that pierce the proximoventral surface of that of *Mononykus* (Perle et al., 1994).

23) Pubic pedicle of ilium slender (Fig. 9). Like other dinosaurs the pubic pedicle of the ilium of *Patagonykus* and *Mononykus* is subtriangular in cross-section and lateromedially compressed. However, in alvarezsaurids the pubic pedicle is elongate and craniocaudally narrow, in contrast with other tetanurines (e.g., *Allosaurus*, Ornithomimidae, *Ornitholestes*, *Deinonychus*, *Archaeopteryx*, Enantiornithes; Madsen, 1976; Osborn, 1917; Ostrom, 1969, 1976b; Walker, 1981; Barsbold & Osmólska, 1990) in which the pubic pedicle of the ilium is craniocaudally thick.

24) Pubic peduncle cranioventrally projected. In Theropoda, ancestrally (e.g., *Compsognathus*, *Allosaurus*, *Ornitholestes*, Tyrannosauridae, Ornithomimidae, *Ingenia*, *Chirostenotes*), the pubic pedicle is anteroventrally oriented. This condition is also seen in *Oviraptor* (AMNH 6517). In *Deinonychus* and *Archaeopteryx* the pedicle clearly surpasses ventrally the level of the ischiac pedicle. Also, the cranial margin of the pubic pedicle is straight and slopes caudoventrally. The caudal margin of the pedicle is more curved caudoventrally increasing the participa-

tion of the ilium in the acetabular surface. In *Deinonychus* (Ostrom, 1969; 1976b) and *Archaeopteryx* (Martin, 1983) the pubic pedicle inclines caudoventrally 115-130° with respect to the longitudinal axis of the iliac blade (where the dorsal margin is assumed horizontal). In Enantiornithes (Martin, 1983) the angle is 140° approximately. In contrast, in *Gallimimus* (Osmólska et al., 1972, pl. 50) and *Ornitholestes* (AMNH 619) the pubic pedicle inclines 50-60° with respect to the longitudinal axis of the blade and in *Tyrannosaurus* (Osborn, 1917) the angle is nearly 70°. *Alvarezsaurus* (Bonaparte, 1991), *Mononykus* (Perle et al., 1993) and *Patagonykus* retained the ancestral condition, with the pubic pedicle cranioventrally oriented. The angulation is not possible to calculate in *Patagonykus*.

The ilio-pubic articulation is too highly modified in *Hesperornis* to discern the inclination of the pubic peduncle. Unfortunately, most of the ilium is lost in *Iberomesornis* (Sanz et al., 1988). In *Apatornis*, and presumably also in *Ichthyornis* (Marsh, 1880), the cranial margin of the pubic pedicle slopes caudoventrally. In *Patagopteryx* neither specimen preserves the pubic peduncle complete, but judging from the available material (Chiappe, 1992) the pubic peduncle seems to be vertical, but not caudoventrally oriented. Caudoventral orientation of the pubic peduncle is also seen in neornithine birds (e.g., *Apteryx*).

25) Fossa for M. cuppedicus absent (Fig. 14). A strongly developed fossa for the femoral protractor M. cuppedicus (Rowe, 1986) is present in the cranioventral corner of the ilium of *Albertosaurus* (AMNH 5458), *Ornithomimus* (USNM 2164), *Deinonychus* (AMNH 3015, MCZ 4371), *Archaeopteryx* (HMN MB 1880/81) and Enantiornithes (Walker, 1981). On the contrary, the lateral surface of the preacetabular blade of the ilium of *Alvarezsaurus* (Bonaparte, 1991), *Patagonykus* (PVPH 37) and *Mononykus* (Perle et al., 1994) is strongly convex dorsoventrally, lacking a fossa for the M. cuppedicus on the ventral margin of the iliac blade. The absence of a fossa for the M. cuppedicus has been interpreted as synapomorphic of the avialian clade formed by *Patagopteryx* and the Ornithurae (Chiappe, 1996) and more recently (Chiappe et al., this volume) as an ambiguous synapomorphy of Metornithes. This uncertainty rises from the unknown condition in *Iberomesornis* (Sanz et al., 1988) and the presence of such an iliac fossa in enantiornithine birds (Walker, 1981). I prefer to interpret the presence of an iliac fossa as primitive for Ornithothoraces (see character matrix in the

Appendix). Consequently, the lack of an iliac fossa for the *M. cuppedicus* is interpreted, with reservations, as an apomorphic character convergently acquired by alvarezsaurids and the clade formed by *Patagopteryx* plus Ornithurae.

26) Supraacetabular crest ending cranially above the pubic pedicle. In *Patagonykus* (PVPH 37) and *Mononykus* (GI N107/6) the supraacetabular crest is almost restricted to the dorsal portion of the acetabular aperture, ending abruptly above the pubic pedicle. A similar condition is present in *Alvarezsaurus* (MUCPV 54) in which the feebly developed supraacetabular crest does not extend over the pubic pedicle of the ilium. This condition contrasts with that present in other theropods (e.g., *Piatnitzkysaurus* MACN-CH 895; *Allosaurus*, AMNH 813; *Archaeornithomimus* AMNH 6576; *Ornithomimus* AMNH 5421; *Albertosaurus* AMNH 5458, 5664; *Ornitholestes* AMNH 619; *Deinonychus* MCZ 4371, AMNH 3015; *Archaeopteryx* HMN MB 1880/81) in which the supraacetabular crest (even in the reminiscent condition present in derived theropods) extends cranially in continuity with the lateral border of the pubic pedicle.

27) Postacetabular blade of ilium with brevis shelf caudolaterally oriented and medial flange ventrally curved (Fig. 9). In *Alvarezsaurus* and *Mononykus* the brevis fossa is present (e.g., a caudoventral basin bounded by a well developed brevis shelf and the medial flange of the ilium; Novas, in press b). The fragmentary nature of the ilium of *Patagonykus* prevents knowledge of this character. The loss of a discrete brevis shelf and fossa apparently constitutes a synapomorphy of the Maniraptora, and its re-acquisition is considered an apomorphic reversal diagnostic of Alvarezsauridae. Interestingly, the ornithothoracine *Patagopteryx* also exhibits a brevis shelf and fossa and, along with alvarezsaurids, constitutes one of the few avialians in which this feature is present (Chiappe, 1996).

28) 'Posterior' trochanter on proximal femur absent. This feature was originally described by Ostrom (1976a, b) for *Deinonychus* and *Archaeopteryx*. After that, the presence of such a prominence was recognised also in Enantiornithes (Chiappe & Calvo, 1994; Chiappe, 1996) and *Sinornithoides* (Russell & Dong, 1993b). The absence of a 'posterior' trochanter in the femur of *Patagonykus*, *Mononykus* and *Alvarezsaurus* is interpreted as an apomorphic reversal.

DISCUSSION

Alvarezsaurids have been recorded at present in Late Cretaceous formations in Patagonia and Mongolia. The recorded taxa are: *Patagonykus puertai* from the Río Neuquén Formation (Turonian; Cruz et al., 1989), *Alvarezsaurus calvoi* from the overlying Río Colorado Formation (Coniacian-Santonian; Bonaparte, 1991; Cruz et al., 1989; Chiappe & Calvo, 1994) and *Mononykus olecranus* documented in the Nemegt Formation (Maastrichtian; Perle et al., 1993, 1994). Chiappe et al. (this volume) have identified bones of species related to *Mononykus* in palaeontological collections previously made by Mongolian and American palaeontologists from the Chinese Iren Dabasu Formation, and the Mongolian Tugrugen Shireh, Bayn Dzak, Ukhaa Tolgod and Barun Goyot (Khermeen Tsav) formations, thought to be Campanian in age (Jerzykiewicz & Russell, 1991; Currie & Eberth, 1993). More recently Holtz (1995: 511) considered '*Ornithomimus*' *minutus* (Laramie Formation, Late Maastrichtian; Marsh, 1892; Weishampel, 1990) as a possible member of the '*Mononykus* lineage'. However the description given by Marsh (1892) is insufficient to support such an assignment, since the features described for the metatarsals of '*O.* *minutus*' are not unique to *Mononykus*, but are also shared by other theropods with the arctometatarsalian condition, as for example Troodontidae, Ornithomimidae, *Avimimus*, Tyrannosauridae (Holtz, 1994). In sum, although presence of alvarezsaurids may be expected in other continents (e.g., North America), reliable records are only known from South America and Asia.

On the basis of the analysis presented above, the common alvarezsaurid ancestor evolved eleven evolutionary novelties (e.g., sacral vertebrae procoelous; caudal sacral centra transversely compressed and sharply keeled ventrally; ungual phalanx of manual digit I stout and robust; pubic pedicle of ilium slender; fossa for *M. cuppedicus* absent; supraacetabular crest ending cranially above the pubic pedicle; haemal arches dorsoventrally elongate; brevis fossa present; 'posterior' trochanter on femur absent; etc.). However, this list of diagnostic traits for the Alvarezsauridae may be larger with the inclusion of several characters, the condition of which is unknown for *Alvarezsaurus*. For example, the stout morphology of the first digit ungual of the manus of *Alvarezsaurus* (see characters A5 & 22) suggests that the first manual digit of this taxon was

powerfully constructed and on the basis of this evidence it is also expected that *Alvarezsaurus* possessed extremely short forelimbs plus all the synapomorphic traits described for *Mononykus* and *Patagonykus* (characters 7-14).

The Patagonian alvarezsaurids *Patagonykus* and *Alvarezsaurus* are more primitive than those from Asia, in accordance with their greater age. However, despite their close geographic and stratigraphic provenance, *Patagonykus* and *Alvarezsaurus* do not exhibit derived characters in common suggesting closer affinities within Alvarezsauridae. On the contrary, there are four features that *Patagonykus* shares with *Mononykus*, exclusive of *Alvarezsaurus*: caudal articular surface of the centra of the last sacral and first caudal vertebrae strongly spherical, sacral vertebrae ventrally keeled, supraacetabular crest present and femoral fourth trochanter present. These features suggest that *Patagonykus* and *Mononykus* are descendants from a common ancestor not shared with *Alvarezsaurus* (Fig. 1).

Discovery of alvarezsaurids less derived than *Mononykus* suggests that the surprisingly modern avialian features present in the later taxon are the result of convergent evolution. Such derived avialian (e.g., ornithothoracine) characters of *Mononykus* are: lack of hyposphene-hypantrum articulation, pubis caudoventrally directed, femoral popliteal fossa distally closed, accessory cnemial crest, fibula not contacting tarsus and astragalar ascending process transversely narrow and laterally displaced. *Mononykus* makes a good case for evolutionary convergence, showing that at least some derived features were acquired more than once in the early evolution of birds. In a more general context, the arctometatarsalian condition of the metatarsals (Holtz, 1994) was acquired at least twice in theropod evolution: once in the Arctometatarsalia clade of theropods (Holtz, 1994) and independently in the derived alvarezsaurid *Mononykus*.

A phylogenetic diagram (Fig. 15) depicting the phylogenetic relationships of the alvarezsaurids, complemented with biochronological information of terminal taxa (e.g., *Patagonykus*, *Alvarezsaurus* and *Mononykus*) and immediate outgroups (e.g., Ornithothoraces), suggests that the origin and diversification of the Alvarezsauridae occurred before the Turonian, probably during Valanginian times (131-138my; Haq & Van Eysinga, 1994). This suspicion about the time of origin of the Alvarezsauridae is in agreement with the currently known biochronology of the Ornithothoraces, the oldest representative of

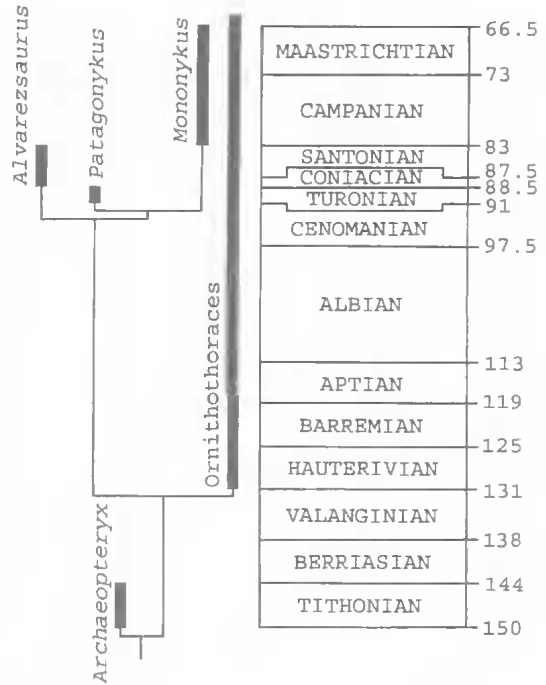


FIG. 15. Phylogenetic diagram depicting phylogenetic relationships of the Alvarezsauridae, complemented with biochronological information.

which (*Sinornis santensis*; Sereno & Rao, 1992) is known from Valanginian rocks. This information indicates that the Alvarezsauridae has a long evolutionary history, the recorded portion of which approximately spans 24.5my; i.e., from Turonian (91my) to Maastrichtian times (66.5my; Haq & Van Eysinga, 1994).

Presence of alvarezsaurids in the Late Cretaceous rocks in Mongolia and Patagonia is puzzling, mainly because alvarezsaurids are one of only two taxa (the other is the Titanosauridae, represented in Mongolia by *Opisthocoelicaudia skarzynskii*; Giménez, 1993; Salgado & Coria, 1993) which are shared by the sharply different Late Cretaceous faunas of South America and Asia (e.g., Bonaparte, 1986b; Bonaparte & Kielan-Jawarowska, 1987; Russell, 1993). There are numerous examples of Cretaceous Gondwanan terrestrial vertebrates which appear to lack close phylogenetic affinities with those from Laurasia. Bonaparte (1986b) and Bonaparte & Kielan-Jawarowska (1987) pointed out the remarkable differences in faunal composition among Laurasian and Gondwanan continents, considering such dissimilarities as a direct consequence of the physical separation of both super-

continental landmasses, which lasted almost the entire Cretaceous period, a time span of 70 to 80my. Russell (1993) has also agreed that several dinosaur taxa evolved separately in Gondwanaland, although he considered that the grouping of terrestrial vertebrates into 'Laurasian' and 'Gondwanan' assemblages was established by Aptian-Albian times.

The shared presence of alvarezsaurids in South America and Asia admits two possible alternatives. One explanation considers alvarezsaurid species from South America and Asia as vicariant taxa descended from an ancestral species widely distributed over northern and southern landmasses; this wide distribution would have occurred before major barriers to overland dispersal among Laurasia and Gondwana were emplaced during Aptian to Cenomanian times (Lillegraven et al., 1979). Following this interpretation, the origin of the Alvarezsauridae must be traced back to Valanginian times, during which Gondwanan and Laurasian continents occupied closer positions than in later times (Scotese et al., 1992). The alternative explanation considers *Alvarezsaurus* and *Patagonykus* as endemic taxa from Gondwana (e.g., South America; Novas & Coria, 1990a; Bonaparte, 1991), which evolved in isolation during Cenomanian to Santonian times; in this context, alvarezsaurids may be interpreted as later emigrants to Asia (via North America?) when continental connections occurred during the Campanian (Bonaparte, 1986b). This later hypothesis agrees with the available fossil record of alvarezsaurids (Fig. 15) and also with palaeogeographic reconstructions (e.g., Lillegraven et al., 1979; Scotese et al., 1992) and palaeobiogeographic interpretations of the evolution of the vertebrate faunas of Gondwana as a whole (e.g., Bonaparte, 1986b; Bonaparte & Kielan-Jawarowska, 1987).

Current geographic documentation of the Alvarezsauridae in South America and Asia suggests that this clade successfully occupied a wide range of environmental conditions. For example, the Neuquén Group, which includes among others the Río Neuquén and Río Colorado Formations, constitutes a succession of sandstones and mudstones deposited under fluvial and lacustrine conditions (Digregorio & Uliana, 1980; Legarreta & Gulisano, 1989). The fauna recorded at the Portezuelo Member of Río Neuquén Formation is made up of gastropods (Cazau & Uliana, 1973), fishes, amphibians, turtles, crocodiles, small ornithischians, small to large theropods and large sauropods (Novas & Coria, 1990b). That of the Río Colorado Forma-

tion is a very rich fauna, including the following taxa (Bonaparte, 1991; Alvarenga & Bonaparte, 1992; Chiappe & Calvo, 1994): notosuchid and sebecosuchid crocodiles, dinilysid booids, sauropods, basal ornithothoracine birds (e.g., *Patagopteryx*, *Neuquenornis*) and ceratosaurian theropods (*Velocisaurus*). In the other extreme of sedimentological conditions in which alvarezsaurids were recorded, are the Asiatic Djadokhta (Tugrugeen Shireh) and Barun Goyot (Khermeen Tsav) Formations, deposited under subaerial conditions of sand dunes, small lakes and streams, in hot and semi-arid climate in areas lacking a permanent fluvial system (Gradzinsky et al., 1977; Osmólska, 1980). It seems to be clear that alvarezsaurids inhabited a wide range of palaeoenvironments (from desertic environments, as those indicated by the sedimentology of the Djadokhta Formation, to more humid conditions as suggested by the fluvial deposits of the Nemegt, Río Neuquén and Río Colorado Formations).

As currently known, Alvarezsauridae includes small forms the size of a turkey (nearly 1m long) such as *Alvarezsaurus* and *Mononykus*, and larger animals, up to 2m, such as *Patagonykus*. They seem to have had a role of predators of small animals, presumably insects (Perle et al., 1994), a suspicion based on the small size of the head and tooth reduction. However, other food items can not be dismissed. Chiappe (1995b) has recently speculated that alvarezsaurids may have used the hand claws to strip bark or perhaps stems from low-growing vegetation. In fact, alvarezsaurids repeat the case of almost uncertain feeding habits as with the ornithomimosaurians, for which carnivorous, herbivorous, or omnivorous habits were variously proposed (e.g., Sanz & Perez-Moreno, 1995). The unusual morphology of the forelimbs is not readily interpreted in reference to behavior and does not help in the elucidation of feeding habits. As commented by Perle et al. (1993, 1994) the sternum and forelimbs of *Mononykus* resemble those of moles mainly due to the presence of a keeled sternum, humerus short and expanded, ulna with elongate olecranon process and stout, slightly curved unguals. These resemblances have been interpreted by Ostrom (1994) as indicative of fossorial habits for *Mononykus*. However, Chiappe (1995b) has dismissed this interpretation. *Mononykus* differs from a mole because in the latter the manus is proportionally large, not only because the number of digits is unreduced, but each digit is robust and a lunate scsamid is added on the medial side of the manus, enlarging its palmar surface. Also, the

body proportions of *Mononykus* sharply contrast with that of digging mammals (e.g., moles and edentates; Hildebrand, 1975), in which the body is compact and the neck, forelimbs and hindlimbs are shortened.

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APPENDIX

TERMINAL TAXA. Character list and taxon-character-state matrix.

The coding of 34 characters used to diagnose three of the six maniraptoran terminal taxa are given below. Some features (e.g., characters M8, M22, M23) have been incorporated in the list below, but have emerged as autapomorphies of some terminal taxa after a cladistic numerical analysis of ingroup relationships was carried out. Data from Bonaparte (1991), Perle et al. (1994), Chiappe et al. (this volume) and Novas (in press a). Scoring: 0, primitive; 1, derived; ?, missing or uncertain.

Patagonykus puertai

P1. Dorsal vertebral postzygapophyses. 0. with lateral margin describing a continuous convex curve in ventral aspect. 1. ventrally sinuous, with a tongue-shaped lateral projection.

P2. Base of the neural arch in postcervical vertebrae. 0. caudally smooth and flat. 1. with a bulge on both sides of the neural canal.

P3. Humeral articular facet of coracoid. 0. transversely wide, being nearly as wide transversely as it is anteroposteriorly. 1. transversely narrow, being as wide transversely as the surface for the articulation for the scapula.

P4. Internal tuberosity of humerus. 0. conical, craniocaudally flattened, or pyramid-shaped. 1. subcylindrical, wider at its extremity rather than in its base.

P5. Humeral entepicondyle. 0. longitudinal prominence on the anteromedial margin of distal humerus, and it is almost anteriorly projected. 1. conical-shaped and strongly projected medially.

P6. First phalanx of manual digit I. 0. ventral surface bounded at both sides by slightly marked ridges on its proximal portion. 1. with proximomedial hook-like processes.

P7. Ectocondylar tuber of femur. 0. robust and elliptical-shaped in distal aspect. 1. transversely compressed, rectangular in distal view.

Alvarezsaurus calvoi

A1. Cervical centra. 0. amphiplatyan or opisthocoealous. 1. amphicoealous.

A2. Cervical postzygapophyses. 0. rectangular in dorsal view, not constricted at their bases, and with

convex dorsal surface. 1. paddle-shaped in dorsal view, dorsoventrally flattened, and with a pair of strong craniocaudal ridges.

A3. Length of distal caudals with respect to proximal caudals. 0. less than 175%. 1. more than 200%.

A4. Scapular blade. 0. craniocaudally wide and distally expanded. 1. slender and reduced.

A5. Ungual phalanx of digit I. 0. with ventral surface transversely rounded or flattened. 1. ventrally keeled.

Mononykus olecranus

M1. Pleurocoels in cervical vertebrae. 0. present. 1. absent.

M2. Sulcus caroticus in cervical vertebrae. 0. absent. 1. present.

M3. Relative position of parapophyses in presacral vertebrae. 0. below the level of the diapophyses. 1. occupying the same level as the diapophyses.

M4. Hyposphene-hypantrum in dorsal vertebrae. 0. present. 1. absent.

M5. Centra of cranial dorsal vertebrae. 0. transversally rounded. 1. strongly compressed transversally, forming a pronounced ventral keel.

M6. Centra of caudal dorsal vertebrae. 0. slightly concave or convex. 1. strongly procoelous, with caudal articular surface hemispherical.

M7. Last sacral centrum. 0. elliptical or transversely compressed in cross-section. 1. extremely compressed transversally, forming a pronounced ventral 'keel'.

M8. Coracoidal shaft. 0. dorsoventral depth not exceeding its anteroposterior width. 1. expanded ventrally, subrectangular in profile, dorsoventral depth more than 130% of anteroposterior width.

M9. Coracoidal shaft. 0. with distal half strongly inflected medially. 1. transversely flat and craniocaudally concave.

M10. Sternal carina. 0. slender. 1. thick.

M11. Ulnar articular surface of the radius. 0. small and restricted to the proximal portion of the radius. 1. extensive.

M12. Carpal articular facet of radius. 0. restricted to the distal portion of the bone. 1. hypertrophied, extended proximally over the caudal and cranial surfaces of the radius.

M13. Proximocaudal process on the first phalanx of digit I. 0. absent. 1. very prominent.

M14. Pubic shaft orientation. 0. almost perpendicular to the iliac surface of pubis. 1. caudoventrally oriented, describing an angle of 70° with the iliac surface of pubis.

M15. Pubic foot. 0. present. 1. absent.

M16. Ischial articular surfaces for ilium and pubis. 0. well developed. 1. extremely reduced.

M17. Femoral distal condyles. 0. separated below popliteal fossa. 1. transversely expanded, nearly confluent below popliteal fossa.

M18. Accessory (medial) entmial crest on tibia. 0. absent. 1. present.

M19. Outer malleolus of distal tibia. 0. craniocaudally narrow in respect to the calcaneum. 1. craniocaudally thick.

M20. Astragalocalcaneal intercondylar groove. *0.* shallow. *1.* deep.

M21. Astragalar ascending process. *0.* transversally wide and not displaced laterally, without overlap onto the lateral margin of distal tibia. *1.* transversally narrow and laterally displaced, with overlap onto the lateral margin of distal tibia.

M22. Femoral trochanteric crest. *0.* anterior trochanter separated from greater trochanter by a cleft. *1.* undivided.

M23. Fibula. *0.* articulates with the tarsus. *1.* does not articulates with the tarsus.

INGROUP CLADES. Character list and taxon-character-state matrix.

The coding and distribution are shown below for 74 characters in six coelurosaur taxa and in two proximate outgroups. All characters are binary. Characters gathered from Gauthier (1986), Russell & Dong (1993a,b), Chiappe (1995, 1996), Chiappe et al. (this volume) and Novas (in prep.).

1. Caudal articular surface of the centra of the last sacral and first caudal vertebrae. *0.* slightly convex. *1.* strongly spherical.

2. Sacral vertebral centra. *0.* transversely rounded or craniocaudally grooved. *1.* strongly keeled ventrally.

3. Femoral fourth trochanter. *0.* present. *1.* absent.

4. Supracetabular crest. *0.* present. *1.* absent.

5. Caudal dorsal vertebrae. *0.* amphiplatyan or amphicoelous. *1.* procoelous.

6. Bicipital tubercle of coracoid. *0.* present. *1.* absent.

7. Forelimbs to hindlimb length. *0.* 40-53%. *1.* less than 26%.

8. Proximal humerus. *0.* major transverse axis of humeral head horizontally oriented with respect to longitudinal axis of the humerus, and internal tuberosity distally placed with respect to humeral head. *1.* major transverse axis of humeral head ventrolaterally inclined with respect to longitudinal axis of the humerus, and internal tuberosity proximally projected.

9. Radial and ulnar condyles of distal humerus. *0.* Separated by an intercondylar groove, and radius and ulna loosely articulated proximally, retaining independent articular surfaces for both radial and ulnar condyles of humerus, respectively. *1.* a single condyle on distal humerus for articulation with radius and ulna, which are tightly appressed proximally, and provided with a cup-shaped proximal articular surface.

10. Olecranal process of ulna. *0.* feebly developed. *1.* strongly developed.

11. Ulnar posterior margin. *0.* sigmoid. *1.* uniformly convex.

12. Carpometacarpus. *0.* slender, elongate, with intermetacarpal space. *1.* massive, short, quadrangular with no intermetacarpal space.

13. Digit I proportions. *0.* transverse dimension subequal to digit II, and longitudinally shorter than digit II. *1.* digit I larger than the remaining digits of the hands.

14. Phalanx I of manual digit I. *0.* with triangular-shaped proximal articular surface, proximoventral sur-

face almost flat, distal ginglymus transversely compressed, and the extensor pit absent. *1.* with B-shaped proximal articular surface, hook-like proximomedial processes, symmetrical distal ginglymus, and deep extensor ligamentary pit.

15. Medial condyle of femur. *0.* transversely narrow and distally convex. *1.* transversely wide and distally flat.

16. Ectocondylar tuber of distal femur caudally projected, well behind the medial distal condyle. *0.* absent. *1.* present.

17. Fibular condyle of femur. *0.* convex or forming a depressed low cone, and slightly surpassing distally the medial condyle. *1.* sharply conical and distally projected respect to the medial condyle.

18. Cervical vertebrae neural spines. *0.* dorsoventrally deep and craniocaudally short. *1.* craniocaudally short and dorsoventrally low.

19. Sacral and caudal vertebrae. *0.* amphiplatyan or amphicoelous. *1.* procoelous.

20. Last sacral centra. *0.* ventrally convex in cross-section, sometimes bearing a longitudinal groove. *1.* transversely compressed and keeled ventrally.

21. Haemal arches of proximal caudals. *0.* dorsoventrally elongate. *1.* dorsoventrally depressed.

22. Ungual phalanx of manual digit I. *0.* dorsoventrally deep, with proximal articular surface elliptical shaped. *1.* stout and robust, dorsoventrally depressed, with proximal articular surface quadrangular.

23. Pubic pedicle of ilium. *0.* craniocaudally wide. *1.* craniocaudally narrow.

24. Pubic pedicle of ilium. *0.* cranioventrally projected. *1.* caudoventrally projected.

25. Fossa for M. cuppedicus on ilium. *0.* transversely wide, with sharp bounding margins. *1.* absent.

26. Supraacetabular crest. *0.* extended cranially in continuity with the lateral border of the pubic pedicle. *1.* ending cranially above the pubic pedicle.

27. Postacetabular blade. *0.* brevis shelf caudolaterally oriented, and medial flange ventrally curved (viz., brevis fossa present). *1.* postacetabular blade vertical, and medial flange strongly reduced, perpendicular to iliac blade (viz., brevis fossa absent).

28. Posterior trochanter on proximal femur. *0.* absent. *1.* present.

29. Vertebral foramen. *0.* small. *1.* wide.

30. Number of caudals. *0.* 35 or more. *1.* less than 25.

31. Neural spines of caudal vertebrae. *0.* present on caudals 1-23. *1.* confined to caudals 1-12.

32. Transverse processes in caudal vertebrae. *0.* reduction begins in caudal 25-16. *1.* in caudal 12 at least.

33. Haemal arches. *0.* become longer than deep behind caudal 17. *1.* behind caudal 10.

34. Mid-caudals prezygapophyses. *0.* elongate. *1.* short.

35. Length of distal caudals. *0.* as long as the proximal caudals. *1.* distal caudals more than 130% of the length of proximals.

36. Ossified sternal carina. *0.* absent. *1.* present.

37(=M8). Coracoidal shaft. *0.* dorsoventral depth not exceeding its anteroposterior width. *1.* expanded

ventrally, subrectangular in profile, dorsoventral depth more than 130% of anteroposterior width.

38. Coracoid shaft with respect to the proximal articular surface for the scapula. *0*. shaft transversely flattened or slightly medially inflected in posterior view. *1*. strongly inflected posteromedially.

39. Dorsal fossa on caudal process of coracoid. *0*. present. *1*. absent.

40. Bicipital tubercle of coracoid. *0*. slightly marked or absent. *1*. strongly developed.

41. Forelimbs. *0*. no more than 53% of hindlimb length. *1*. exceeding 75% of hindlimb length.

42. Forelimbs. *0*. not exceeding 75% of hindlimb length. *1*. 86% or more of hindlimb length.

43. Shape of the internal tuberosity (= bicipital tubercle) of humerus. *0*. conical. *1*. craniocaudally compressed and longitudinally elongated.

44. Radius/humerus length ratio. *0*. no more than 0.71. *1*. 0.76 or more.

45. Carpometacarpus. *0*. carpals and metacarpals unfused. *1*. carpometacarpus present.

46. Distal carpal. *0*. proximodistally flattened. *1*. semilunate.

47. Digit I proportions. *0*. digit I ends at level of mid-length of phalanx 2, digit II. *1*. digit I ends at level of mid-length of phalanx 1, digit II.

48. Posterodorsal margin of ilium. *0*. straight. *1*. curves ventrally in lateral view.

49. Posterior end of ilium. *0*. dorsoventrally deep, squared or rounded. *1*. dorsoventrally low and sharply pointed.

50. Antitrochanter on ilium. *0*. slightly marked. *1*. prominent.

51. Pubic apron. *0*. transversely wide and proximodistally long. *1*. strongly reduced transversely and restricted to the distal 1/3 of the pubic length.

52. Pubis. *0*. cranioventrally oriented. *1*. caudoventrally oriented respect to the pubic pedicle of ilium.

53. Pubic apices. *0*. in contact. *1*. not in contact.

54. Obturator process on ischium. *0*. present. *1*. absent (the cranioventral margin of ischium is almost straight).

55. Ischial to pubic length. *0*. elongate ischium, slightly shorter than pubis or femur. *1*. nearly half of pubis or femoral length.

56. Medial condyle of femur. *0*. dorsoventrally deep. *1*. dorsoventrally depressed.

57(=M22). Femoral trochanteric crest. *0*. anterior trochanter separated from greater trochanter by a cleft. *1*. undivided.

58. Adductor fossa and associated craniodistal crista of distal femur. *0*. present, prominent. *1*. reduced or absent.

59. Tibia-femur proportions. *0*. tibia no more than 15% longer than the femur. *1*. tibia 25% longer than the femur.

60(=M23). Fibula. *0*. articulates with the tarsus. *1*. does not articulate with the tarsus.

61. Articulations of quadrate and squamosal. *0*. quadrate articulates only with squamosal, the latter contacting both the quadratojugal and the postorbital. *1*.

quadrate articulates with both prootic and squamosal, and the latter contacting neither the quadratojugal nor the postorbital.

62. Serration of teeth. *0*. present. *1*. absent.

63. Teeth crown-root constriction. *0*. absent. *1*. present.

64. Ulnar distal condyle. *0*. transversely compressed and craniocaudally extended approximately in the same plane as humero-ulnar flexion-extension. *1*. subtriangular in distal view, with a dorsomedial condyle, and twisted more than 54° with respect to proximal end.

65. Calcaneum. *0*. posteroventral projection present. *1*. strongly reduced.

66. Pubic distal foot. *0*. cranial projection present. *1*. absent.

67. Prominent ventral processes of cervico-dorsal vertebrae. *0*. absent. *1*. present.

68. Large, rectangular ossified sternum. *0*. absent. *1*. present.

69. Terminal processes of ischia. *0*. in contact. *1*. not in contact.

70. Fibular tubercle for M. iliofibularis. *0*. craniolaterally projected. *1*. laterally, caudolaterally, or caudally directed.

71. Proximal and distal humeral ends. *0*. twisted. *1*. expanded in nearly the same plane.

72. Pelvic elements. *0*. unfused. *1*. fused or partially fused.

73. Proximal end of fibula. *0*. excavated by a medial fossa. *1*. nearly flat.

74(=M4). Hyposphene-hypantrum in dorsal vertebrae. *0*. present. *1*. absent.

TAXON CHARACTER STATES.

Ornithomimidae

00000 00000 00000 00100 00000 00000 00000 00000
00000 00000 00000 00000 00000 00000 00000 0000

Tyrannosauridae

00000 00000 00000 00000 00000 00000 00000 000?0
00000 00000 00000 00000 00000 00000 00000 0000

Deinonychus

00010 00000 10000 00000 10010 01100 11101 01000
10110 10100 01001 10100 00001 00000 0000

Archaeopteryx

00110 000?0 10000 0?000 10010 011?1 11111 01111
11110 11110 01001 ?0110 01101 100?? 00??

Ornithothoraces

00110 00000 10000 00?00 10010 01111 11111 11111
11111 11111 11110 01111 1111? 11111 1111

Mononykus

11001 11111 01111 11111 01101 10011 11110 10010
00001 10101 11110 11111 11110 11111 1111

Patagonykus

11001 11111 01111 11?11 ?1101 1?01? ???10 ??010
?00?1 1???1 110?? 101?0 ???10 0???? ?010

Alvarezsaurus

0011? ????? ???? ?1111 011?1 100?? 10111 ??0??
????? ?110? ????? ?0??0 ???00 ????? ????